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PACIFIC SCIENCE

A QUARTERLY DEVOTED TO THE BIOLOGICAL AND PHYSICAL SCIENCES OF THE PACIFIC REGION

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Report on Hawaiian Polyclads

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A History of the Binomial Classification of the Polynesian Native Dog

KATHARINE LUOMALA[1]

THIS IS A SURVEY of attempts from the last quarter of the eighteenth century to the present to give a binomial classification to the Polynesian native dog. Taxonomic interest has been expressed mainly by German and British natural scientists. Most of them, having neither seen a living Polynesian dog of unquestioned native breed nor studied skeletal material from a dog presumed to be of native breed, have had to depend on a few generalized descriptions by explorers and settlers. Presented here are the taxonomists' classifications and theories, the descriptions that they have cited, and the probable sources and dependability of any of their unacknowledged information about the appearance of the Polynesian native dog.

This paper results from my interest, mostly anthropological and mythological, in the Polynesian native dog. Polynesians in New Zealand, the Tuamotus, and the Hawaiian Islands narrate variants of a myth that the demigod Maui-of-a-thousand-tricks transformed a man he hated into a dog, the first known to them and a symbol of abhorred traits like gluttony, laziness, and incest. A story, entirely different from this, that Samoans and Tongans tell, of how Maui died when he attempted to kill a cave-dwelling, man-eating dog, is probably a post-European composition since the dog was apparently absent from western Polynesia at the time of European discovery (Luomala, 1958). Polynesians had ambivalent attitudes toward the dog, for it was both a symbol of the social outcast and a symbol of prestige that through its varied uses increased the status of its owner (Luomala, 1960).

The dog was present at the time of European discovery of Polynesia in only a few archipelagoes. The Tuamotus, Society Islands, Hawaiian Islands, and New Zealand had dogs which I believe they did not get from any *known* European explorers and which may actually have been descendants of dogs introduced into the eastern Pacific by the Pacific islanders themselves. No dependable evidence has been found of the dog's presence in western Polynesia at the time of first European contact. Indicative of the intricacies of the question of the pre-European distribution of the dog is the fact that the first European reference to seeing a dog in Polynesia was in 1606 at a Tuamotuan atoll, perhaps Anaa, where the Quiros expedition met an old lady carrying a little white or speckled dog and wearing a gold and emerald ring! Also in certain other islands like Tonga, for example, no dogs existed but the natives recognized and called by the name of *kuri*, the most common Polynesian word for dog, the dogs on board Captain James Cook's ships (Luomala, 1960).

Only studies of skeletal remains of dogs from archeological sites definitely established as pre-European by radiocarbon dating or other means will provide more information than we now have on the native dog. Only in the Hawaiian Islands, New Zealand, and the Marquesas is such work going on at present. The Marquesans apparently had no live dogs at the time of European discovery in 1595, but recent finds in 1956 of remains of dogs in what appear to be pre-European sites on the western coast of Nukuhiva Island point to their former presence in the Marquesas (Shapiro, 1958: 269).

I have never located any information as to what finally happened to the Tahitian dog that George Forster of Cook's second expedition mentions was brought back to England. There is no further word on its fate in England or what disposition of its hide and skeleton was eventually made when it died. It was one of two of the Society Islands dogs aboard ship that had recovered from an experiment on them at "Mallicollo" (Malekula, New Hebrides) with Malekulan arrow poison. Later the dogs, like some other domestic animals and a pet bird aboard

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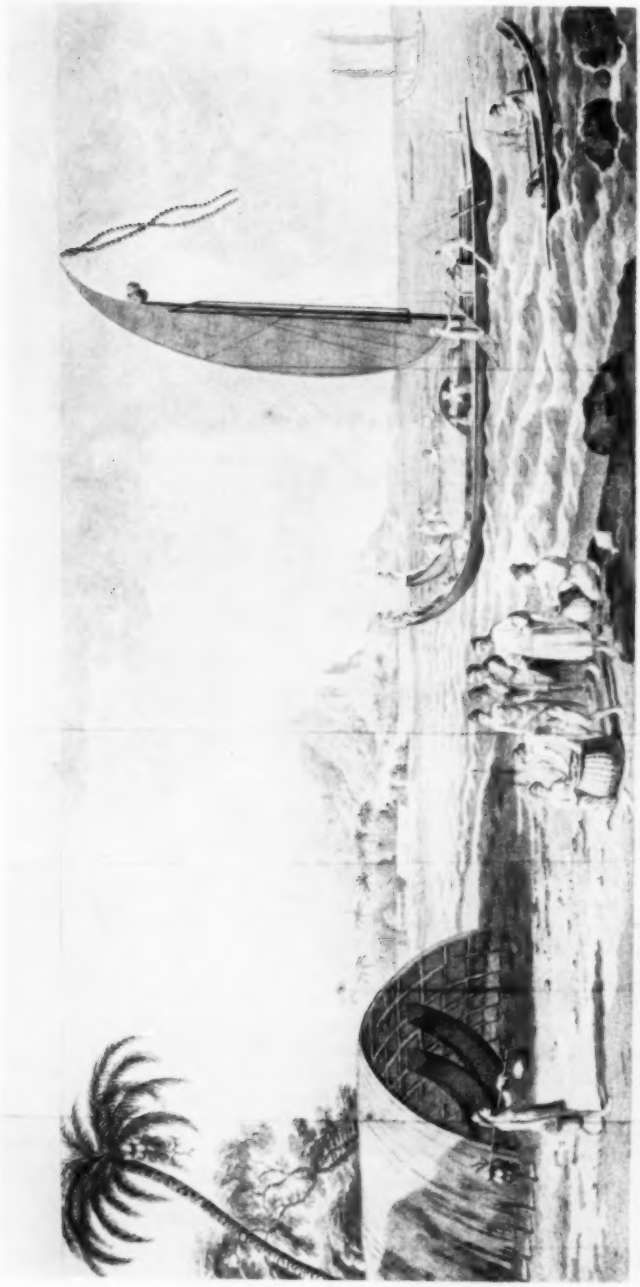

FIG. 1. "A view in the island of Ulietea with double canoe and a boat house" (Hawkesworth, 1773, II : pl. 3). Raiatea, Society Islands, on Captain Cook's first voyage. The dog is aft on the large double canoe. The head of a horned cow is visible forward.

and some of the crew, suffered agonies from eating poisonous fish. Of the dogs George Forster writes (1777, II: 244), "One of these poor creatures was doomed to be a martyr, being the same upon which we tried the Mallicollese arrows; however he luckily got the better of both these attacks, and was brought to England."

ILLUSTRATIONS

Artists of the eighteenth and nineteenth centuries have depicted island dogs. The drawings from the nineteenth century, however, usually show dogs that are obviously European or mixed European and native. Even in the earlier drawings one must consider the possibility that a pet of foreign origin from the European ships has got into the scene. Most often the artists show the dogs in canoes, like family pets determined to go for a ride.

Two illustrations by Sydney Parkinson, artist on Cook's first expedition, show dogs in canoes in the Society Islands. One (Hawkesworth, 1773, II: pl. 3) is "A view in the island of Ulietea with double canoe and a boathouse," and shows a dog sitting in a canoe at Ulietea (Raiatea) which is also transporting a horned cow from the European ship. Another sketch (Hawkesworth, 1773, II: pl. 4) is "A view of the island of Otaheite with several vessels of that island"; and shows a dog sitting contentedly by a youth with a long-poled net.

Two unidentified photostats at Bishop Museum of sketches of canoe scenes in the Society Islands, obviously of the eighteenth century, and done by British artists, to judge from the titles, do not appear in any published collections of illustrations that accompany the voyages. Dogs appear in the scenes. One scene, with the title "Double Canoes. Tipaerua," probably written in by the artist, clearly shows a dog in one of the canoes. The other scene with the title "Canoe of Ulietea," also written in by the artist, shows a child on the deck of a double canoe clasping a dog with a very pointed muzzle. The original drawings, I later learned, are at the British Museum, from which I then obtained fine photographs of the two drawings and of the particular sections showing the dogs. The Keeper of the Department of Manuscripts states "that the information given by the catalogue of additions is as follows: 'A collection of drawings by A. Buchan, S. Parkinson and J. F. Miller, made in the countries visited by Captain Cook in his first voyage (1768–71), also of prints published in John Hawksworth's Voyages of Biron, Wallis and Cook, 1773, as well as in Cook's second and third voyages (1762–5, 1776–80).'" Since to my knowledge the drawings do not appear in any of the published accounts, I am inclined to believe that they were made by one of the three artists named above in the countries visited by Cook on his first voyage in 1768–1771. In other words, they probably belong to the same series as the two named above which Hawkesworth used in writing up the account of Cook's first voyage.

Published plates by John Webber, artist on Cook's third expedition, also depict dogs. One scene (Cook, 1784: Atlas, pl. 14) of "The reception of Captain Cook in Hapaee," Hapai, Tonga, shows a lean dog at the lower right of the picture. Another scene (Cook, 1784: Atlas, pl. 31) is "A view of Huaheine," Society Islands, and shows a man kneeling on the deck of a double canoe near the boathouse and perhaps holding still the dog in front of him so that the artist can sketch it.

Louis Choris (1822), in a drawing owned by the Honolulu Academy of Arts and previously unpublished (Bishop Museum Negative 20599), shows a Hawaiian scene with two dogs in the foreground. The larger dog because of its size and flopping ears does not fit the customary description of the native dog; the smaller dog

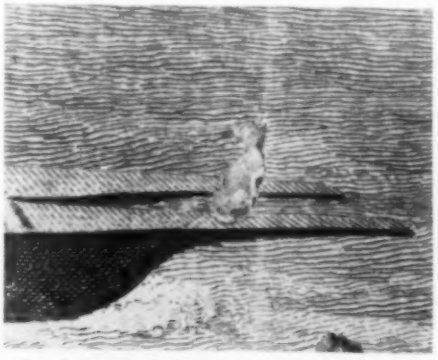

FIG. 2. Detail of dog shown in double canoe in Figure 1 at Raiatea, Society Islands.

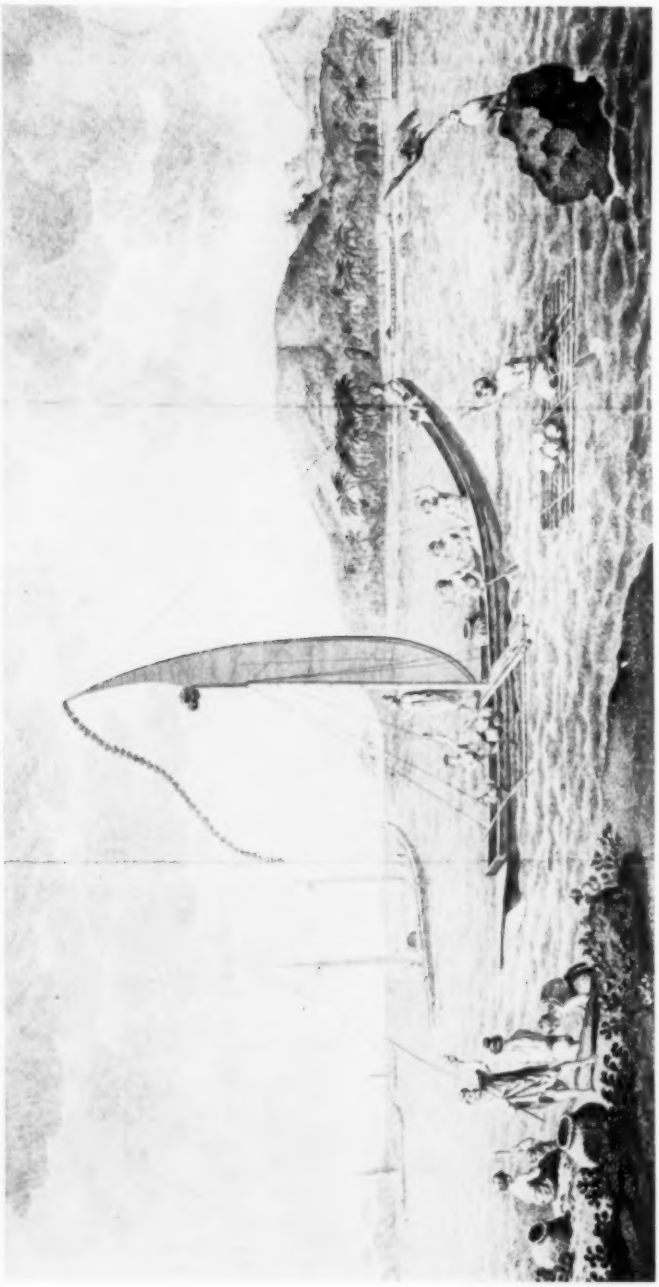

FIG. 3. "A view of the island of Otaheite with several vessels of that island" (Hawkesworth, 1773, II : pl. 4). Tahiti, Society Islands, during Captain Cook's first voyage. The dog is sitting below the boy in the prow. As usual, a seagoing rooster is also in the picture.

is nearer the type. Vaillant (Album, No. 45; Bishop Museum Negative 20588) in "Vue de Honolulu. Iles Sandwich" done in the mid-1830's shows a dog with a Hawaiian couple. Dogs depicted by artists in later volumes look increasingly like European breeds.

The Dominion Museum, Wellington, New Zealand, has kindly sent a photograph of a specimen (B. 3527) often described, though questionably, as of the pre-European breed of dog. Dr. T. Barrow writes to me from the Museum that ". . . the history of the specimen is inadequate, and the ancestry of the dog doubtful. . . . It was collected at Waikawa, but there are several Waikawas in New Zealand, and we are not sure which place is referred to. The collector was Anderson. We may take it that it is not one of the two dogs caught during the time of Sir George Grey's office in this country."

Sir George Grey, former Governor-General of New Zealand, sent to the British Museum in the last half of the nineteenth century (Hector, 1876: 244) the hide and skeleton of one of two dogs thought to be of the native breed. Among the long-time residents of New Zealand who interested themselves in what the native breed had looked like and whether any traces remained, W. Colenso (1877), who had thoroughly criss-crossed North Island between 1834 and 1854, declared that he had never seen a true Maori dog and considered these later dogs, such as the one Sir George sent to the Museum, to be wild dogs not of the native breed. A large problem not taken up in my study is the evaluation of an extensive literature, mostly from New Zealand, describing and discussing nineteenth-century specimens that are regarded by some writers as belonging to the pre-European native breed or breeds. The stuffed specimen at the Dominion Museum was often figured in Elsdon Best's (1924, I: 433) writing as a native breed.

George Forster compared the New Zealand native dog with the shepherd's cur depicted by Buffon (1755, V: pl. 28), and H. G. L. Reichenbach (1836: 46, pl. 72) sketches a most imaginative reconstruction of the appearance of *Canis tahitiensis*.

A Papuan with his dog hunting wild pigs that swim near the canoe was sketched in the last quarter of the eighteenth century (Forrest, 1779: 59, pl. 11).

What seems to be the first depiction of the Australian native dog, the dingo, appeared in 1789 (Phillip, 1789: pl. 45, facing p. 274) with the publication of a sketch of a female from New South Wales, which Governor Phillip had sent to England as a present that eventually came into the possession of the Marchioness of Salisbury at Hattfield House. Another specimen in England was owned by Mr. Lascelles. The London zoo also had some. A description is given in a later section of my paper because of the frequent references to post-European mixtures of the dingo and the native dog of New Zealand.

Among Hawaiian petroglyphs are representations of dogs. Figure 22 shows a section of petroglyphs in Nuuanu Valley, Honolulu.

FOUR PRIMARY EIGHTEENTH-CENTURY SOURCES

Scientists interested in classifying Polynesian native dogs cite most often three or four of the several statements about dogs made by J. R. Forster and his son George, natural scientists who accompanied Cook on his second voyage to the Pacific from 1772 to 1775. The Forsters' accounts, together with those of the New Zealand dog by Crozet in 1772 and of the Hawaiian dog in 1779 by Lieutenant James King (later Captain King), are the first extensive, but not the first, references to the dog in the literature

FIG. 4. Detail of dog in Figure 3. The long muzzle is clearly evident. The ears seem to be flopped forward.

about Polynesia. Both Crozet's and King's accounts are largely overlooked by taxonomists. None of the four primary describers attempts any classification.

Superficial and incomplete as the four descriptions are, they are the best available because they definitely are about the native dog. Later descriptions must always be suspect because during the last quarter of the eighteenth century the native dog increasingly lost its identity through cross-breeding with dogs which European ships had picked up in ports around the world and taken to the islands. The Forsters and others had pet dogs, some of European or other foreign breeds, others of native breeds, and still others of mixed native and foreign origin. Captain Cook bought many native dogs either to be eaten on his ships or to be given as gifts to Polynesian and Melanesian chiefs who had no dogs (Luomala, 1960).

The generalized description of the native dog by J. R. Forster (1778: 189) which is most often cited or paraphrased by classifiers follows:

> The dogs of the South Sea isles are of a singular race: they most resemble the common cur, but have a prodigious large head, remarkably little eyes, prick-ears, long hair and a short bushy tail. They are chiefly fed with fruit at the Society Isles; but in the low isles and New Zealand, where they are the only domestic animals, they live upon fish. They are exceedingly stupid, and seldom or never bark, only howl now and then; have the sense of smelling in a very low degree, and are lazy beyond measure: they are kept by the natives chiefly for the sake of their flesh, of which they are very fond, preferring it to pork; they also make use of their hair, in various ornaments, especially to fringe their breast plates in the Society Isles, and to face or even line the whole garment at New Zealand. . . .

Taxonomists also often cite two of George Forster's descriptions, one of the New Zealand dog and the other about that in the Society Islands. These zoologists, most of them German, quote from the German translation of Forster's journal, which first appeared in English. The reference in the German edition (1778, I: 165) differs from the English edition (1777, I: 377) only in omitting a reference to the texture of the dog's hair being rough.

According to George Forster, in June, 1773, some of the New Zealand Maoris visiting Cook's ship had dogs in their canoes:

> A good many dogs were observed in their canoes, which they seemed very fond of, and kept tied with a string, round their middle; they were of a rough long-haired sort, with pricked ears, and much resembled the common shepherd's cur, or count Buffon's *chien de berger* (see his Hist. Nat.). They were of different colours, some spotted, some quite black, and others perfectly white. The food which these dogs receive is fish, or the same as their masters live on, who afterwards eat their flesh, and employ the fur in various ornaments and dresses. They sold us several of these animals, among which the old ones coming into our possession became extremely sulky, and refused to take any sustenance, but some young ones soon accustomed themselves to our provisions.

The various editions of Buffon's work use different illustrations of the sphepherd's cur but the sketch (see Fig. 17) in the first edition (1755, V: pl. 28, following p. 300) is probably the one known to Forster. It is usually difficult to know what variety of dog a writer has in mind when he likens the Polynesian dog to a shepherd's cur, barbet, pomeranian, turnspit, poodle, dachshund, terrier, fox-dog, or Asiatic pariah dog. These popular terms tend to be differently used at different periods and in different countries and localities. Moreover, changes largely resulting from artificial selection and breeding occur as time passes after a writer has made his comparison. Also, popular terms follow no classificatory system. Terms like shepherd's cur and turnspit refer to the dog's function in a culture. A writer comparing the Polynesian dog to a barbet or a pomeranian is thinking mostly, it seems, only of the long hair characteristic of these two breeds. Seeking to discover what each breed looked like at the time the comparison was made leads into a fascinating maze because the name of each breed has an associated literature so controversial that one concludes that the correct term for a writer about dogs is not scientist but dogmatist. George Forster, then, is exceptional in referring to a particular illustration of the European breed with which he compares the New Zealand dog.

George Forster's description of the dogs of

the Society Islands is identical in both his German (1778, I: 285–286) and English (1777, I: 377–378) editions, but the former is more often cited by the German classifiers. Of an exploratory walk that he and Dr. Anders Sparrman took on Huahine, Society Islands, in September, 1773, he states:

On this walk we saw great numbers of hogs, dogs, and fowls. The last roamed about at pleasure through the woods, and roosted on fruit-trees; the hogs were likewise allowed to run about, but received regular portions of food, which were commonly distributed by old women. We observed one of them in particular, feeding a little pig with the sour fermented bread-fruit paste, called mahei; she held the pig with one hand, and offered it a tough pork's skin, but as soon as it opened the mouth to snap at it, she contrived to throw a handful of the sour paste in, which the little animal would not take without this strategem. The dogs in spite of their stupidity were in high favour with all the women, who could not have nursed them with a more ridiculous affection, if they had really been ladies of fashion in Europe. We were witnesses of a remarkable instance of kindness, when we saw a middle aged woman, whose breasts were full of milk, offering them to a little puppy which had been trained up to suck them. We were so much surprised at this sight, that we could not help expressing our dislike of it; but she smiled at our observation, and added, that she suffered little pigs to do the same service. Upon enquiry, however, we found that she had lost her child, and did her the justice amongst ourselves to acknowledge that this expedient was very innocent and formerly practiced in Europe. The dogs of all these islands were short, and their sizes vary from that of a lap-dog to the largest spaniel. Their head is broad, the snout pointed, the eyes very small, the ears upright, and their hair rather long, lank, hard, and of different colours, but most commonly white and brown. They seldom if ever barked, but howled sometimes, and were shy of strangers to a degree of aversion.

Early classifiers, being interested in description rather than in causes of variation in the Polynesian dog, ignore the Forsters' opinions on why Polynesian dogs acted differently from European dogs and what effects such external factors as food, care, education, and climate had on them. These opinions are first shots, broad and random, at an important problem. Almost 75 years were to pass before the classifiers began to take a dynamic view about the peculiarities of the Polynesian dog.

J. R. Forster (1778: 200–201, 372) writes that the individuals in the animal kingdom in the South Seas show less variety than those in the plant kingdom:

Domestication, the great cause of degeneracy in so many of our animals, in the first place, is here confined to three species; the hog, dog, and cock; and secondly, it is in fact next to a state of nature in these isles. . . . The dog being here merely kept to be eaten, is not obliged to undergo the slavery, to which the varieties of that species are forced to submit in our polished countries; he lies at his ease all the day long, is fed at certain times, and nothing more is required of him; he is therefore not altered from his state of nature in the least; is probably inferior in all the sensitive faculties to any wild dog (which may perhaps be owing to his food), and certainly, in no degree, partakes of the sagacity and quick perception of our refined variety.

He also notes that the hogs and dogs "are very prolific, thrive in the fine climate amazingly well, and soon come to maturity. . . ."

George Forster (1777, I: 235, 243), after remarking that "it is owing to the time we spend on the education of dogs that they acquire those eminent qualities which attach them so much to us . . .," suggests that the fish or vegetable diet has altered canine disposition to make Polynesian dogs stupid. Such education as they get, he says, has "perhaps likewise grafted new instincts" that have led New Zealand dogs to eat the dead of their own species and the remains of their masters' cannibal feasts.

Until 1922 when George M. Thomson incorporated it into his monograph on New Zealand plants and animals, the following description by Crozet was generally overlooked by classifiers outside of New Zealand. Of the dogs that he saw in 1772 in New Zealand, Crozet (Roth, 1891: 76) writes:

They have absolutely no other domestic animal than the dog. The dogs are a sort of domesticated fox, quite black or white, very low on the legs, straight ears, thick tail, long body, full jaws but more pointed than that of the fox, and uttering

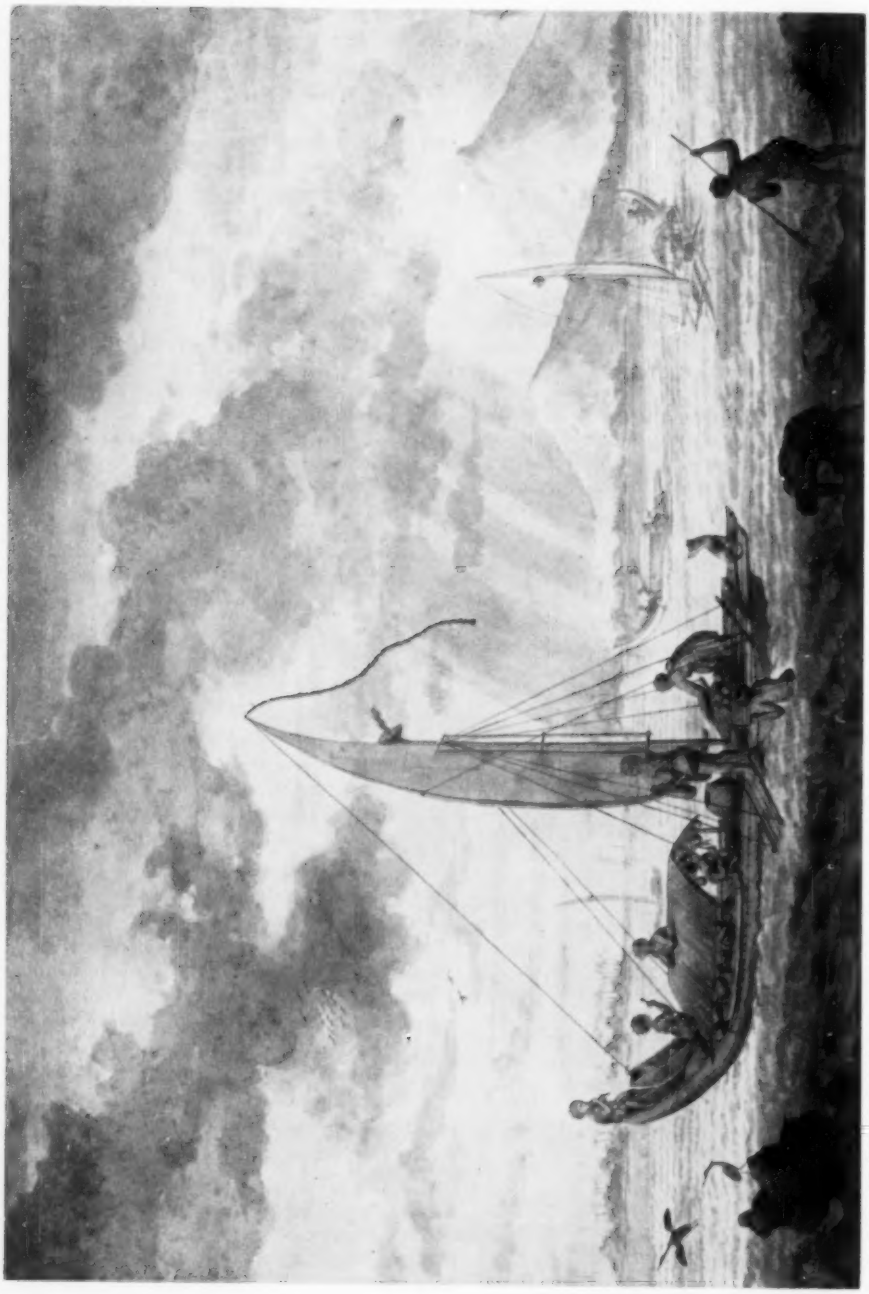

FIG. 5. "Double canoes. Tiparua." Society Islands, probably during Captain Cook's first voyage. A previously unpublished sketch in the British Museum. A dog is sitting on the aft deck.

the same cry; they do not bark like our dogs. These animals are only fed on fish, and it appears that the savages only raise them for food. Some were taken on board our vessels; but it was impossible to domesticate them like our dogs, they were always treacherous, and bit us frequently. They would have been dangerous to keep where poultry was raised or had to be protected; they would destroy them just like true foxes.

The fourth primary describer of Polynesian dogs during the eighteenth century is Lieutenant King. After Cook's death King's journal was used to complete the official journal of the third expedition. Although King saw living native dogs in abundance before any known European contact had occurred with the Hawaiian Islands, which Cook's third expedition discovered, his account was little known to taxonomists. Without citing his source, F. L. Walther in 1817 seems to be the first to use it. In King's description written in March, 1779, the interest shown in the causes of the peculiar behavior of the dogs perhaps reflects that of the Forsters. For the first time an observer mentions the achondroplasic condition of the legs. Crozet appears to be the first to mention the long body. King writes (Cook, 1784, III: 118):

> The dogs are of the same species with those of Otaheite, having short crooked legs, long backs, and pricked ears. I did not observe any variety in them, except in their skins; some having long and rough hair, and others being quite smooth. They are about the size of a common turnspit; exceedingly sluggish in their nature, though perhaps this may be more owing to the manner in which they are treated than to any natural disposition in them. They are, in general, fed and left to herd with the hogs; and I do not recollect one instance in which a dog was made a companion, in the manner we do in Europe. Indeed, the custom of eating them is an insuperable bar to their admission into society; and, as there are neither beasts of prey in the island, nor objects of chase, it is probable that the social qualities of the dog, its fidelity, attachment, and sagacity, will remain unknown to the natives. The number of dogs in these islands did not appear to be nearly equal in proportion to those in Otaheite. . . .

There are as many different descriptions of turnspits as there are describers, because "turnspit" was the name for any dog in Europe or the British Isles that was taught to run around inside a treadmill wheel to work a roasting spit. Whether or not it was a distinctive breed, and if so, of what kind and of what ancestry, makes for an interesting argument. Some who consider it a distinctive breed identify it as a descendant of the short-legged pariah dog; others perhaps think only of a line of descendants of some capable and admired local turner of a roasting spit, whose pups were sought as likely to be equally teachable, capable, and physically suitable. In general, a medium-sized, sturdy, teachable dog was used. Sometimes the turnspit is described as having a long back, short legs, straight or crooked, and fur that was shaggy and sometimes spotted. An early English reference to mongrels that were trained to turn the spit or to dance to drums and a lyre is dated 1570 (Davis, 1949: 34). The last was used in Wales and Germany about 1870, according to Vesey-Fitzgerald (1948: 728–729), who shows a sketch of a turnspit; when suitable dogs became scarce, a dog, which alternated with a companion, was paid about 6 d. a day at the most.

PENNANT AND SOME EARLY GERMAN TAXONOMERS

The famous "Third Edition" of Thomas Pennant's *History of Quadrupeds* is the often unacknowledged source used by later zoologists

FIG. 6. Detail of dog in Figure 5. This is the best picture I have found of what seems to be a native Polynesian dog: long muzzle, oblique eyes, prick ears, large head, stocky body, short legs, scraggly tail, patchy color, coarse hair, with only the alert look alien to descriptions.

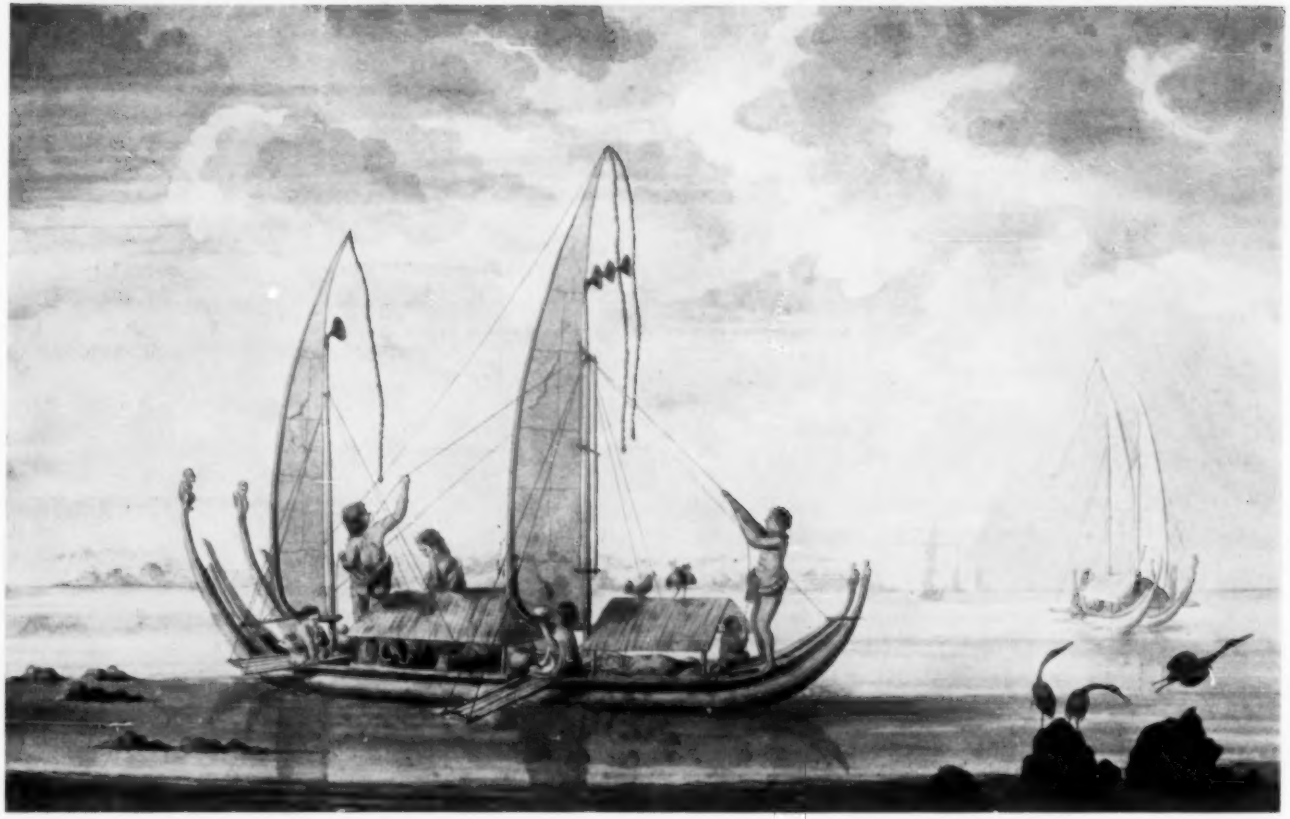

FIG. 7. "Canoe of Ulietea." Raiatea, Society Islands, probably during Captain Cook's first voyage. A previously unpublished sketch in the British Museum. A boy at the left clutches what looks like a dog.

for information, secondary in origin though it is, about Oceanic dogs. J. M. Bechstein, who translated this edition into German in 1799, adds a little interpretation which scholars using his translation quote. Neither Pennant nor Bechstein gives a binomial classification of the Polynesian dog.

Pennant is probably the first to make fairly explicit two problems which still recur and are still unsolved. The first centers about whether or not there was more than one variety, or breed, of Polynesian dog, and if so what the distinctive characters of each were. Pennant distinguishes two varieties on the basis of the length and quality of the hair. The second problem concerns the relationship, if any, of the native dogs in the entire Pacific area to each other and to the Eurasiatic dogs, and the determination of the center of their geographical distribution to the islands. Pennant, discussing Polynesian, Australian, and New Guinea dogs, regards them (if I interpret his often ambiguous statements correctly) as derived from New Guinea, and separable into three, perhaps four, varieties. They are the New Holland (Australian) dingo, the Polynesian dog resembling the shepherd's cur, the Polynesian dog resembling the barbet, and the New Guinea dog which he regards as ancestral to at least the Polynesian "currish fox-like dog" and perhaps to others. Pennant's statements are so ambiguous, however, that each reader interprets them differently.

Pennant (1793, I: 243–244; Bechstein, 1799, I: 258–160) writes as follows:

> Dogs (brought originally from New Guinea), are found in the *Society Islands, New Zeland,* and the *Low Islands;* there are also a few in New Holland. Of these are two varieties.
>
> 1. Resembling the sharp-nosed pricked-ear shepherd's cur. Those of *New Zeland* are of the largest sort. In the *Society Islands,* they are the common food, and are fattened with vegetables, which the natives cram down their throats, as we serve turkies, when they will voluntarily eat no more. They are killed by strangling, and the extravasated blood is preserved in *Coconut* shells, and baked for the table. They grow very fat, and are allowed, even by *Europeans* who have got over their prejudices, to be very sweet and palatable.
>
> But the taste for the flesh of these animals was not confined to the islanders of the *Pacific Ocean.* . . .
>
> 2. The *Barbet,* whose hair being long and silky, is greatly admired by the *New Zelanders* for trimming their ornamental dress. This variety is not eaten. The islanders never use their dogs for any purposes but what we mention; and take such care of them as not to suffer them even to wet their feet. They are excessively stupid, have a very bad nose for smelling, and seldom or never bark, only now and then howl. The *New Zelanders* feed their dogs entirely with fish.
>
> The Marquesas, Friendly Islands, New Hebrides, New Caledonia, and Easter Isle, have not yet received those animals.

For New Guinea, Pennant cites as his source Captain Thomas Forrest (1779: 97, "table" 11). What Pennant calls a table is given as a plate by Forrest. Forrest, a visitor on the New Guinea coast in the early part of 1775, twice (1779: 97 and 103) remarks on the native dogs around "Dorry" (Daru). He observed natives setting out in boats with two or three "fox-looking dogs . . . a dog they call Naf." The dogs were used to hunt wild pigs that in swimming from islet to islet sometimes held on to the tail of the preceding pig. Forrest writes on seeing men on another occasion setting out in their boats to go pig-hunting, "In each boat was generally a small fox looking dog," and then in his plate11 (Figs. 19, 20) he depicts such a scene. Forrest gives no further data about the appearance of the dog.

FIG. 8. Detail of Figure 7 showing boy clutching an animal that looks like a dog. Or is it a pig?

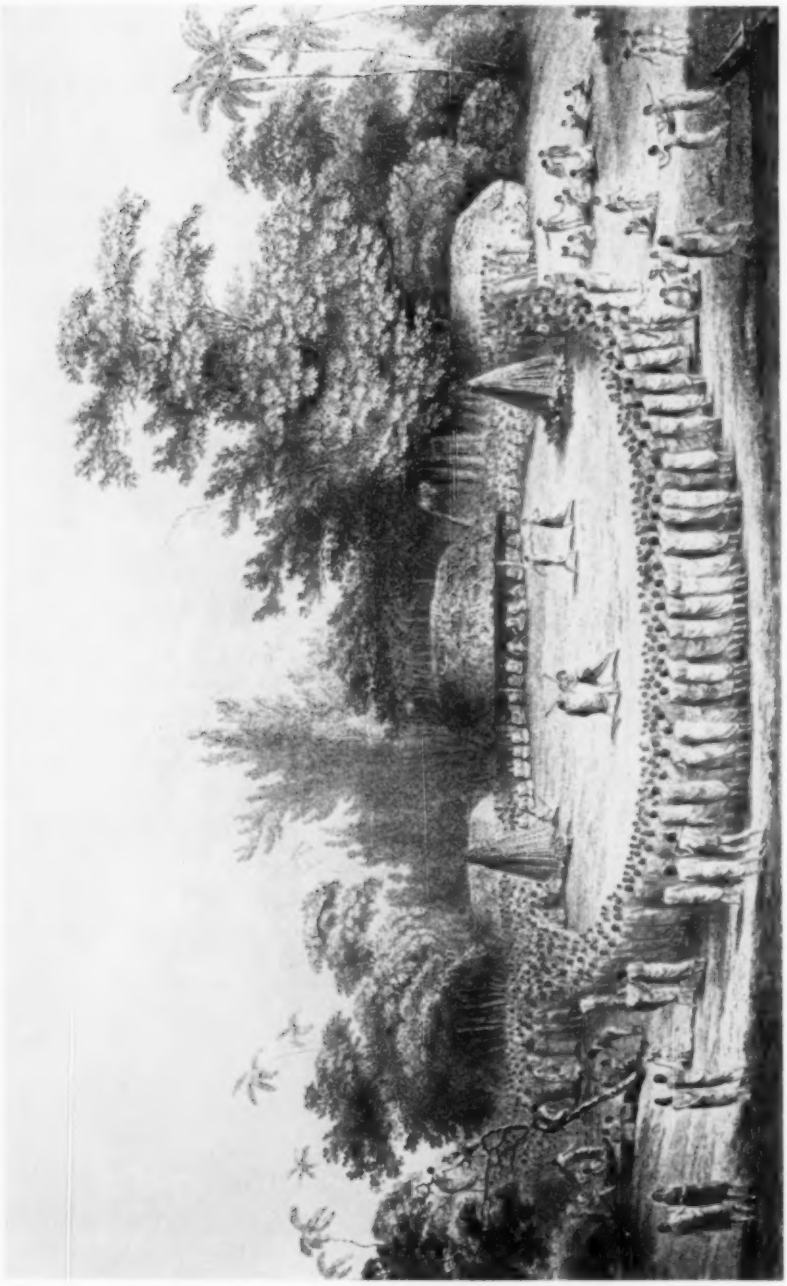

FIG. 9. "The reception of Captain Cook, in Hapaee" (Cook, 1784 : Atlas, pl. 14). Hapai, Tonga Islands, on Captain Cook's third voyage. A scrawny dog is at the lower right outside the circle of people.

Pennant considers (1793, I: 143) that "New Guinea must have originally supplied with dogs those south sea islands which . . . (have them)." New Guinea, he continues, was probably the "Mother of Lands," the homeland, as native priests also claim, of men, dogs, hogs, poultry, and rats; here, Pennant states, is found the "same species of hog, and the currish fox-like dog" as in Polynesia. If Forrest is his direct source, rather than inspiration, for this conclusion I do not find the reference anywhere in Forrest's account of his voyage. Pennant's puzzling introductory statement given earlier seems to mean that both Polynesian and Australian dogs came from New Guinea.

Pennant gives a description of the "New Holland dog" (1793, I: 247).

Pennant's undesignated authorities for his other statements about the Polynesian dog are undoubtedly members of Cook's expeditions, especially the Forsters, and occasionally Cook himself. Cook, on his first visit to the Society Islands, describes (Hawkesworth, 1773, II: 152–153) how delicious a young fat dog is and how to cook a dog in native fashion after it has been strangled and its blood caught in a coconut shell. Others on that expedition, Sydney Parkinson for example, also write, not always favorably, about their first experience in eating dog meat. Contrary to Pennant, George Forster states that the Maoris ate dogs, and that Society islanders forcibly fed baby pigs, not dogs. That they similarly fed puppies is likely but Forster does not say so. Also contrary to Pennant, dogs were not common food in the Society Islands (J. R. Forster, 1778: 372).

I have not located Pennant's source about the long-haired New Zealand dog being protected against getting its feet wet. The statement may be a misinterpretation or extension of the meaning of Forster's reference to the Maoris having their dogs with them in their canoes. Pennant's description of the Maori dog's hair as silky, a detail that Walther quotes from Pennant, is unsupported by the Forsters; the younger Forster says the opposite. However, the latter in a statement (1777, II: 40), that classifies apparently overlook, mentions that the dogs at Tiookea (Takaroa), Tuamotus, had "fine long hair of a white colour." That the Polynesian dog was "fox-like" may echo Cook's journal (1784, I: 153) in which the New Zealand dog is called "a sort of fox-dog." Crozet makes the same point but his description was overlooked. Pennant's list of islands that at the time of European discovery lacked dogs comes from J. R. Forster (1778: 188); Captain Cook introduced dogs into some of these islands.

Bechstein's German translation of Pennant's work inserts the adjective "Australische" to describe the barbet. The adjective, absent from Pennant's English edition, is puzzling because it is not clear whether Bechstein uses the term to mean "Australian" or "southern." Early writers usually call Australia New Holland so that an adjective referring to the country would not be "Australische." It is not derived from the classification of the Polynesian dog as *Canis australis* because, so far as I can determine, that does not appear until later.

Adding to the confusion, F. L. Walther (1817: 23), who depends largely on Bechstein's translation and a little directly on George Forster, applies the name "Australische Hund" to his *Canis familiaris villaticus, meridionalis*. This is not the dog Pennant likens to the barbet but the variety he compares with the shepherd's cur. Perhaps Walther purposely reverses Pennant's two varieties to get back closer to Forster, the original source. Referring to Bechstein (1799, I: 258) and George Forster (1778, I: 286) as his sources, Walther states that his subvariety *meridionalis* is found in the Society and the Sandwich islands, also in New Zealand, and a

FIG. 10. Detail of the scrawny dog in Figure 9.

FIG. 11. "A view of Huaheine" (Cook, 1784 : Atlas, pl. 31). Huahine, Society Islands, on Cook's third voyage. In the canoe at the left a man is kneeling and holding a dog still.

few in New Holland. These dogs, he adds, had short legs, long backs, pricked ears, an occasional howl but no bark. They were shy towards strangers and stupid. They were eaten. Walther drops the Low Islands (the Tuamotus are probably meant) from the list and substitutes the Sandwich (Hawaiian) Islands. The references to the Sandwich Islands and to the dogs being long-backed and short-legged (he does not include the fact that the legs were often crooked) indicate that Walther, although he does not give his source, was probably familiar with King's description. He probably includes New Holland with the islands having his *meridionalis* because he interprets Pennant's ambiguous introductory statement to refer only to the first of the varieties described.

Walther has another Polynesian subvariety which he calls *Canis familiaris villaticus, novae Zeelandiae*, the New Zealand dog. He describes it from sources that he gives as Bechstein (1799, I: 258) and George Forster (1778, I: 165). This dog, he says, resembled a shepherd's dog, and had long silky hair, pricked ears, and different colors. It was found in New Zealand where it was fed almost exclusively on fish and kept only for its hide, from which festive attire was made. It was not eaten. It was very stupid, had a poor sense of smell, and rarely barked but only howled now and then.

Two more South Pacific dogs classified by Walther (1817: 21–24) are the Australian dingo, *Canis familiaris villaticus, novae Hollandiae*, and the "fox-like dog of New Guinea," *Canis familiaris villaticus, novae Guineae*. He gives as sources Bechstein (1799, I: 260) and Forrest's ("Forster") German edition (1782: 121, 126). An error in his book which regularly gives Forster when Forrest is meant is continued by later writers.

Walther obviously then makes explicit and gives binomial classifications to four Pacific varieties that he distinguishes and that are not so explicit in Pennant's account. Moreover, he (1817: 21–24) puts all four in the same larger classification *villaticus* as four Old World breeds, to make a total of eight "national breeds" in *C. familiaris domesticus*. The Old World breeds in *villaticus* are the common, black, long-haired German house dog with curled-over tail, *germanicus* (one of Walther's lists inserts the Lapland dog next); the Kalmuk dog, *calmuccorum;* the Pyrrenes dog, *pyrenaicus;* and that of Pomerania, *pomeranus*. Walther leaves no doubt that he regards the Pacific dogs as belonging to the same genus, species, and variety *(Canis familiaris villaticus)* as the Old World breeds of domesticated house dogs. So far as I can determine, he is the first even to attempt to classify the Polynesian dog by genus and species.

H. G. L. Reichenbach (1836: 46, pl. 72) does not describe the dog he classifies as *Canis otahitensis*, but his sketch (Fig. 18) shows some dogs whose most remarkable feature is a long, flowing tail like that of a horse. The source of the artist's inspiration is not stated. Perhaps Reichenbach describes the dog and cites his authority on page 141 in his "Naturg. Raubth." (perhaps, in full, *Naturgeschichte Raubsäugethiere*) which I have not seen but which Leopold J. Fitzinger (1867: 400–401) quotes without giving the complete title. Fitzinger states that Reichenbach gives two other classifications of the Polynesian native dog. They are *Canis familiaris orthodotus* and *Canis familiaris orthotus otahitensis*. The spelling of the sub-species varies. Reichenbach (1836: 22) classifies the dingo both as *Canis Dingo* or, according to Fitzinger (1867: 817), *Canis familiaris orthotus Dingo* ("Naturg. Raubth.": 147, 354), and as *Chrysaeus Australiae* ("Naturg. Raubth.": 366).

Consideration of Fitzinger's own classifications will be deferred until later.

FIG. 12. Detail of Figure 11 to show a long-legged, flop-eared, spotted dog with a long muzzle and short, half-curved tail.

C. G. A. Giebel (1859: 844), who classifies the dogs of New Zealand, Society Islands, and Sandwich Islands as *Canis familiaris otahitensis*, does not describe or figure them or give his sources. His geographical distribution echoes that of Walther in dropping the Low Islands from Forster's original list and substituting the Sandwich Islands. Giebel's classification resembles that of Reichenbach. I have not seen Giebel's later books. He classifies (1859: 842) the dingo both as *Canis familiaris* and as *Lupus familiaris*.

THE MID-NINETEENTH CENTURY MAORI DOG AND THE DINGO

Giebel and Reichenbach each gives one classification of the dingo (also called warrigal) that excludes it from the genus *Canis*. This is a reminder that Blumenbach's classification in 1780 of the native dog of Australia (absent from Tasmania) as *Canis familiaris dingo* was sometimes questioned. Some classifiers did not consider the dingo a true dog. Others, who did, agreed on practically only one point, according to Frederic Wood-Jones (1925: 352), which is "That the Dingo is some sort of a dog." Many of the opinions, he observes (p. 350), "rest on nothing more than a mere haphazard statement founded on no proper examination of the characters of the animal." The same can be said about the Polynesian *Canis*.

It is already evident that one cannot talk about the Polynesian dog without mentioning the dingo and other native dogs of the Pacific. The following summary of some material on the New Zealand dog also shows why even this cursory survey of the Polynesian dog cannot completely ignore the dingo. However, the name of the dingo is linked only with that of the New Zealand dog, principally because more has been written about the Maori dog than about other dogs of Polynesia.

FIG. 13. A Hawaiian scene (Honolulu Academy of Arts, Bishop Museum Negative 20599) by Choris, 1820, previously unpublished. The large dog at the left looks foreign. The smaller dog by the pig somewhat recalls the odd creature in Figures 7 and 8.

By the early part of the nineteenth century the New Zealand dogs were mongrelized. The description in 1820 by Captain Bellingshausen (1945: 215) is the last, and in fact the only one in the nineteenth century, which inspires even a little confidence that it is about a native dog. He mentions "rather a small breed of dog . . . not large," with "thick tail, erect ears, a broad muzzle, and short legs." Soon packs of wild dogs became such a nuisance and danger that European settlers imported dogs from Australia to use in hunting these wild packs. Some of the imported dogs may have been dingos, or had a dingo strain, to add to the existing mixture. In Australia the dingo itself was such a nuisance to settlers that it had a price on its head. Although it too had crossed with introduced dogs, Wood-Jones (1925: 355–356) considers that pure dingos still existed in the twentieth century even in those cattle districts settled the longest.

Consideration of Wood-Jones' comparison of dingo crania with those of certain other carnivores will be deferred until later. A general description (Le Souef and Burrell, 1926: 89–93, pl. 9, a photograph) will provide a basis for the discussion to follow. The dingo, which howls but does not bark, has an elongated head with a pointed nose and well-developed canine teeth. It has straight toes with blunt claws, five on the forelimbs and four on the hind limbs. Its rather long, coarse hair is tawny except for greyish underfur. The top of the head and the dorsal sections are generally darker, the under parts lighter; the tip of the brush-tail, the feet, and the chest are generally white. The cheeks and the outside of the legs are whitish-tawny. Regional color variations include white dogs with some tawny shadings, and black dogs with tan points and face. The head and body measure 715 mm.; the tail, 350 mm.; the height at the shoulder, 530 mm., and at the ear 90 mm. Wood-

FIG. 14. "Vue de Honolulu. Iles Sandwich" (Vaillant, Album, No. 45, Bishop Museum Negative 20588). The mid-1830's in Honolulu. A dog follows a Hawaiian couple.

Jones (1926: 349–350, 355) describes the ears as large, pointed at the tips, carried erect, and fringed with hairs; tails of wild dogs droop, those of pet dogs are usually carried erect; coats vary in color, with both black and red mentioned by early observers. Wood-Jones gives 1500 mm. as the length of the head and the body, but the tail is about the same length as that mentioned above; height is not given.

A description of the dingo, which is often quoted at second- and third-hand in early zoological studies, appears in connection with the sketch of the dingo female referred to earlier (Fig. 21). The description (Phillip, 1789: 274–275) identifies the animal as "Canis. Dog. Dog of New South Wales," and continues:

> The height of this species, standing erect, is rather less than two feet: the length two feet and a half. The head is formed much like that of a *fox*, the ears short and erect, with whiskers from one to two inches in length on the muzzle. The general colour of the upper parts is pale brown, growing lighter towards the belly: the hind part of the fore legs, and the fore part of the hinder ones white, as are the feet of both: the tail is of a moderate length, somewhat bushy, but in a less degree than that of the fox: the teeth are much the same as is usual in the genus, as may be seen in the top of the plate where the animal is represented.
>
> This species inhabits *New South Wales*. The specimen from which the annexed plate was

FIG. 15. Detail of Figure 14 to show a spotted dog with prick ears and a long tail.

taken, (a female) is now alive in the possession of the *Marchioness of Salisbury*, at *Hattfield-House*, and was sent over as a present to Mr. *Nepean*, from Governor *Phillip*. It has much of the same manners of the dog, but is of a very savage nature, and not likely to change in this particular. It laps like other dogs, but neither barks nor growls if vexed and teized; instead of which, it erects the hairs of the whole body like bristles, and seems furious: it is very eager after its prey, and is fond of rabbits or chickens, raw, but will not touch dressed meat. From its fierceness and agility it has greatly the advantage of other animals much superior in size . . . [examples of its nearly killing a French fox-dog and an ass]. . . .

A second of these is in the possession of Mr. *Lascelles*, of which we have received much the same account in respect to its ferocity; whence it is scarcely to be expected that this elegant animal will ever become familiar.

The dingo is a hunter which runs down its prey before killing it. Its hunting ability contrasts with that of the Polynesian native dogs, of which only the Maori dogs may in pre-European times have hunted wild ground birds. Some Maori dogs were trained to hunt. This hunting ability of some Maori dogs is mentioned in native traditions and post-European descriptions but there are no references to the custom by the earliest explorers to give complete confidence in these other sources of information (Luomala, 1960).

Although J. S. Polack, who travelled in New Zealand between 1831 and 1837, frequently mentions the dogs he encountered and classifies them, he nowhere specifically describes one or more of them. He writes (1838, I: 308):

Of quadrupeds, indigenous to the country, there are none. The karárahé, or dog (Canis Australis), which, when young, is known as *kuri*, has been an inhabitant some two or three centuries. A tradition yet exists of his having been given to the natives, in times remote, by a number of divinities, who had made a descent on these shores.

This sagacious animal has dwindled down to the lowest grade of his interesting family, which may be easily accounted for from the stinted allowance that has come to his share for many generations.

He also writes (*op. cit.*, p. 310), "The former name of a dog in the country was *pero*, which in some measure substantiates the supposition of Juan Fernandez having visited the country, *pero* signifying a dog in the Spanish language."

Polack discursively alternates between eulogies of the devotion of New Zealand dogs to their owners and denunciations of them as mongrels and "curs of the lowest degree in the scale of animal creation" and "the greatest pest in the country" (1836, I: 66, 74, 135, 141, 155, 156, 230, 308–314, 389, 400; II: 254). The behavior of the barking, pugnacious, and sheep-killing dogs that Polack saw suggests that few if any were of the pre-European native varieties or unmixed with European breeds.

Ernest Dieffenbach (1843, II: 184), also familiar with New Zealand of the early nineteenth century, quotes Polack and adds further observations:

The dog of the natives is not the Australian dingo, but a much smaller variety, resembling the jackal, and of a dirty yellowish colour. It is now rarely met with, as almost the whole race of the island has become a mongrel breed. A native dog of New Zealand is not a sufficiently powerful animal to do harm to domestic sheep, but it is different with the introduced and mongrel dogs, mostly bull-terriers or bloodhounds, which are savage pig-dogs although with men they are great cowards. In want of better sport they hunt young birds, and to this cause the scarcity of many indigenous birds must be ascribed. The natives also call the dog sometimes 'Pero' (Spanish): they have a tradition that their ancestors brought the dog with them when they first peopled New Zealand. Is it not probable, from the Spanish name, that the dog was brought to them by navigators of that nation before the time of Tasman?

Tasman, it will be recalled, reported the discovery of New Zealand in 1642 though he did not land.

Dieffenbach (II: 45–47; I: 417) repeats this information with slight variations and additions. The color of the dog is "reddish brown," the ears are "long and straight." The animal "rather resembles" the jackal whereas the dingo is like the wolf in size and shape.

John Edward Gray (who styled himself "F.R.S., British Museum") contributes a section on fauna to Dieffenbach's book. The part on the

dog begins with Dieffenbach's long paragraph quoted above. Yet despite Dieffenbach's flat denials that the dingo and the native New Zealand dog are the same, Gray (Dieffenbach, 1843, II: 184) identifies the New Zealand dog as "The New Holland Dog.—Canis familiaris Australis, Desm.; Canis Dingo, Blumenb." Without giving his source he adds that the dog is said to have been introduced from Australia. His dissatisfaction with his identification is hinted in his comment that "It would be interesting to institute an accurate comparison between these animals [Maori] and an Australian specimen." Gray also quotes Polack about the dog having been in New Zealand for two or three centuries.

Contrary to the impression given by Gray, A.-G. Desmarest (Gray abbreviates his name as Desm.) does not describe the Polynesian dog or equate the dingo with it. He writes (1816, VI: 454–455) about the "New Holland dog" and cites F. Cuvier's description of a specimen taken to France by F. Péron. Desmarest is also quoted on the dingo by William Youatt (1846: 41–43), who also writes of the Polynesian dog but without linking it to the dingo. Youatt refers to the Polynesian dog as "Canis Australis-karárehé, New Zealand dog," terms which, with other general statements, point to Polack as his unacknowledged source.

The question of the relationship of the dingo and the New Zealand dog is also raised by the contemporaries of Gray and Dieffenbach in New Zealand. By the nineteenth century the popular identification of any dog, wild or domesticated, in Polynesia with any native dog, either of Polynesia or of any other Pacific area like Australia, was guesswork. Nonetheless, arguments were common (and are easily started even now) as to whether any native dogs unmixed with European dogs survived, what native dogs

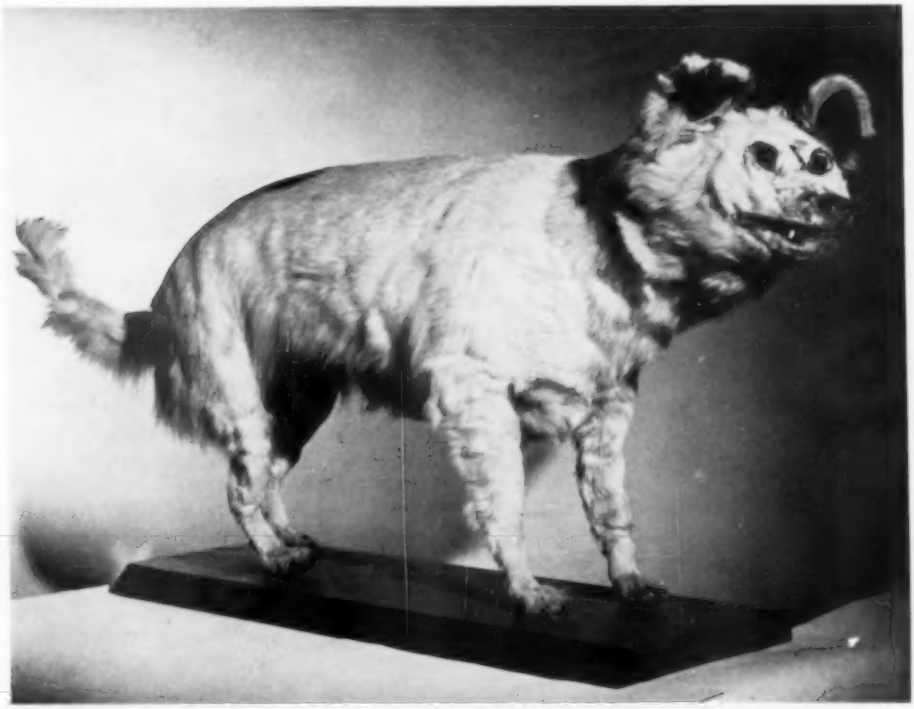

FIG. 16. Stuffed dog (B. 3527, Dominion Museum, Wellington, New Zealand) sometimes regarded as representative of the Maori native dog. Photo by Dominion Museum.

looked like, and what traits survived either in wild dogs or in domesticated dogs in native villages. Descriptions derived from natives were quoted, telling what they thought their ancestors' dogs looked like. To R. Taylor (1870: 604) the New Zealand dog or "canis familiaris kuri . . . was small and long-haired, of a dirty white or yellow colour, with a bushy tail." This dog, Taylor had learned from natives, had been brought when their ancestors first came to the islands. Taylor considers it "not improbable, however, that they found another kind already in the country, brought by the older Melanesian race, of a larger size, with long, white hair and black tail . . . said to have been very quiet and docile, and was known by the name pataka tawhiti, both these are now quite lost in the host of introduced ones." No support occurs for the theory of Melanesians having preceded Polynesians in occupying New Zealand. A. Reischek (1924: 100–101) writes about "Canis Maori" on receiving a dogskin mat said to have been made from hides of native dogs. The term "native" becomes increasingly vaguer in meaning as time passes; applied to dogs it might mean those of any breed that a Polynesian native owned.

FIG. 17. "Le chien de berger" (Buffon, 1755, V: pl. 28). The shepherd's cur that is compared with the Maori and the Australian native dogs.

George M. Thomson (1922: 64–70), who classifies the New Zealand dog as *Canis familiaris*, has assembled information about its appearance from the time of Crozet and Forster to the twentieth century. The material comes from early visitors, later travel writers and ethnographers, contributors to New Zealand newspapers and scientific journals, and personal correspondents. Included are statements indicating that arguments occurred which linked the names of the Australian dingo and the New Zealand native dog. For example, a certain settler writes (Thomson, 1922: 68) that in 1858 among the wild dogs that he killed were some yellow ones that "looked like a distinct breed. They were low set, with short pricked ears, broad forehead, sharp snout, and bushy tail. Indeed those acquainted with the dingo professed to see little difference between that animal and the New Zealand yellow wild dog." Like many other pioneers, this settler, in hunting wild dogs that harried people and livestock, had the help of his "kangaroo dog," imported from Australia for hunting wild dogs. Not stated in the accounts is the breed of the kangaroo dog, whether dingo or mongrel.

None of the explorers of the seventeenth and eighteenth centuries mentions transporting native dogs for exchange between Australia and Polynesia, so that, as far as is known, crossbreeding in European times of dingos and Polynesian native dogs did not take place till after the eighteenth century. However, Polynesian dogs, it will be recalled, were introduced into dogless New Caledonia and New Hebrides by Captain Cook on his second expedition; and, in the first quarter of the nineteenth century, R. P. Lesson and P. Garnot (Duperrey, 1826, I: 123), natural scientists on the Duperrey expedition, abandoned at Port Jackson, Australia, the native dogs they had bought in New Ireland. Later I shall return to their comparison of these and other Melanesian and New Guinea dogs with the dingo. For the present, it is enough to note that although Europeans transported local dogs

around the Pacific in the early days of European travel, no one happens to mention any exchange of dogs between Australia and Polynesia that might have led to a mixture of local breeds.

Those who regard the dingo and the Polynesian dog as close kin ignore, however, the theory that the dingo may not be a true dog. Therefore, they do not raise the inevitable question, "Was the Polynesian native dog a true dog?" In fact, no one interested in the Polynesian dog appears to have expressed doubt that it belongs in *Canis*, except perhaps Elizabeth Morey (Im Thurn and Wharton, 1925: 188), who lived at the beginning of the nineteenth century in Tongatabu (where Cook, it will be remembered, introduced native dogs and the people also got some later from Fiji). She writes that "the natives hold in high estimation the flesh of a small sized animal of the dog kind, which many prefer to the finest fish." And, again in contrast to the dingo, the question has not been raised as to whether the Polynesian dog's wild ancestor was nearest a wolf, jackal, fox, or other carnivore.

The polyphyletic theory, that the various races of domestic dogs derive not only from the wolf but from the jackal, fox, and coyote, had famous followers like I. G. Saint-Hilaire and Charles Darwin, although the latter (1897, I: 216) felt none too convinced. The polyphyletic theory still has some followers, although the evidence offered has rested less on studies of the less plastic features like teeth and skulls than on superficial, modifiable traits like, for example, the carriage of the ears and tail or the quality and color of the coat. Discussions of the polyphyletic or monophyletic origin of the domestic dog usually bypass the Polynesian native dog but not the dingo; yet, as has been noted, in the mid-nineteenth century European settlers in New Zealand debated whether or not the dingo of Australia and the native dog of New Zealand were related.

Wood-Jones (1926) compares a series of 20 dingo skulls, selected at random from a collection of corpses, with 10 other series or individuals of what are probably mostly European breeds and also compares these series with crania of wolves, foxes, and jackals. Tables and sketches accompany his study. His purpose to determine the place of the dingo led to conclusions that supported both Blumenbach's classification of the dingo as *Canis familiaris* and Cuvier's belief that the dingo is "the most primitive true dog." Wood-Jones finds that the dingo's teeth, especially the upper carnassial, are relatively more nearly the size and form of those of the wolf than are those of any other breed of dog studied. Long isolation in Australia apparently has stabilized the resemblances to the teeth of the wolf that Wood-Jones regards as ancestral to domesticated dogs. The teeth of wolves and dogs differ in certain significant characteristics from those of the jackal and the fox. The dingo, Wood-Jones suggests, probably came with man by a sea route to Australia. A fact derived from his comparison that particularly impresses him is that the series of dingo skulls shows "a degree of uniformity far greater than that seen in any series of skulls of dogs of any breed" (1926: 355).

Wood-Jones' study is regarded as "the most compelling account favoring the northern wolf as the original ancestor of the dog" (Vevers, 1948: 5). N. A. Iljin (1941: 410), after an 8-year genetical study in Russia of the offspring of hybrids produced by crossing a female black mongrel sheep dog and a male wolf, gray in color and caught wild, also suggests "the *possibility* of the origin of the various races of *Canis familiaris* from a single wild species, viz. *C. lupus*." These two studies have had much to do with discrediting the polyphyletic theory.

CLASSIFICATIONS BY FITZINGER AND SMITH

In the mid-nineteenth century, L. J. Fitzinger and Charles Hamilton Smith, though chronicling the increasing mixture between Polynesian dogs and foreign dogs, show some interest in the

FIG. 18. An imaginative artist's idea of *Canis tahitiensis* (Reichenbach, 1836 : 46, pl. 72).

same questions that the Forsters and King raise about the pre-European origin of the causes of what are regarded as either degenerate or primitive traits in the Polynesian dog. Neither Fitzinger nor Smith had specimens to study.

Among the peculiar traits of the Polynesian dog were its inability to bark, its predominantly indolent disposition (except perhaps in New Zealand), its erect ears, long back, short and crooked legs, comparatively large head with small eyes, and pointed muzzle. More interest has been shown in identifying the presence of these traits in mongrels believed to contain native strains than in determining the origin of the traits. The traits (except perhaps the laziness) when present, whether in dogs of Polynesia or of other parts of the world, are called primitive; that is, they are regarded as traits shared with the wild ancestor of the dog whatever it is thought to have been, whether wolf, fox, or other animal. Sometimes these same traits are called degenerate; the implication occasionally is that degeneration has occurred from a more advanced form toward the primitive form. Both the idea of primitiveness and of degeneracy toward primitiveness seem to be mixed in the views of the Forsters and King.

That the same perhaps is true of the views of Smith and of Fitzinger, although the former refers to degeneracy and poor breeding and the latter speaks of acclimatization, is suggested by their famous contemporary's discussion of the origin of breeds among dogs.

Charles Darwin (1897, I: 40) writes of the deteriorating effects of diet and climate on imported dogs, which have led to their "reversion to a primordial condition which many animals exhibit . . . when their constitutions are in any way disturbed." Darwin also considers the effect of what are now called mutations:

> Some of the peculiarities characteristic of the several breeds of the dog have probably arisen suddenly, and, though strictly inherited, may be called monstrosities; for instance, the shape of the legs and the body in the turnspit of Europe and India. . . . A peculiarity suddenly arising, and therefore in one sense deserving to be called a monstrosity, may, however, be increased and fixed by man's selection . . . the most potent cause of change has probably been the selection, both methodical and unconscious, of slight individual differences,—the latter kind of selection resulting from the occasional preservation, during hundreds of generations, of those individual dogs which were the most useful to man for certain purposes and under certain conditions of life.

Pictures on Egyptian monuments from about 3400 B.C. to 2100 B.C. show dogs, he points out, which include a turnspit with short crooked legs resembling the existing variety. He also refers to a description of an Indian pariah dog with similarly short, crooked legs. Such legs are common enough in various animals, Darwin finds (1897, I: 17), so he rejects the Egyptian counterpart of the "monumental animal as the parent of all our turnspits." In other words, a breed like the turnspit, sometimes compared with the Polynesian native dog, might arise through mutations more than once in different parts of the world. However, the latter-day genetical studies on dogs by C. R. Stockard (1941) have shown that the achondroplasic factor is dominant in inheritance. Therefore, the dogs with the deformed-looking bandy legs and peculiar muzzles pass on these traits by Mendelian laws of inheritance to their descendants. When achondroplasic features inhibit natural functioning, the breed becomes extinct.

Mongrels in native Polynesian villages that exhibit peculiarities reminiscent of those the native dog is thought to have had are generally assumed to have some native-dog ancestry. The possibility that at least some of these mongrels might be mixtures only of European breeds that, through degeneration or mutation, have come to duplicate independently the primitive or degenerate traits of the native dog has not been considered, except perhaps with the regard to the trait of nonbarking. All howling wild dogs are not kin to the indigenous dogs in breed, for, according to common knowledge, European dogs which become feral may lose the ability to bark and resort only to howling. They recover their bark if they return to a domesticated life.

C. H. Smith (1845, XIX: 210) writes of what he calls the poi dog (*C. Pacificus*), the *ilio* of the Hawaiians and the *uri-mahoi* of the Tahitians: "In form this variety bears marks of decrepitude: the head is sharpened at the muzzle, the ears erect, the back long, the limbs crooked;

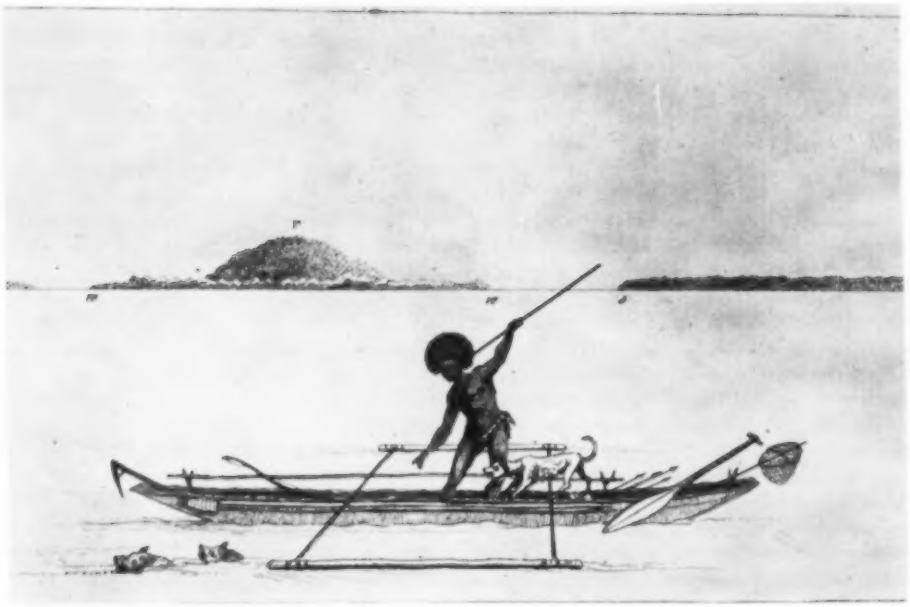

FIG. 19. A Papuan and his dog hunting wild pigs (Forrest, 1779 : 59, pl. 11).

the hair is smooth, but retains its primitive livery of tan or rusty ochre colour." The silent and lazy dog, Smith continues, subsists on a vegetable diet of breadfruit and of poi made from taro. Entirely reserved for the table, the dog is a real delicacy to the natives. In the Society Islands, Smith adds, it is now mixed in breed, but in the Hawaiian Islands the "pure breed of Poe dog is better protected." Mentioning the skinned dog that Frederick Bennett saw suspended over a restaurant door in Honolulu in the 1830's, Smith states that the poi dog is the size of a terrier, with dull expression, tail straight or slightly curled, brown livery, feeble but shrill bark, and in disposition gentle and indolent. The poi dog, he concludes, "in aspect presents the mixed forms of a fox-dog, turnspit, and terrier." It is just as badly shaped, he says, as the turnspit which is long-backed, heavy-bodied, and either straight- or crooked-legged; and like the turnspit and the pariah dog it shows poor breeding, degeneracy, and malformation.

Smith (1845, XIX: 210–211, 296), who like most writers on the native dog depends on written descriptions, gives various classifications of Polynesian native dogs. He distinguishes apparently between the "poe dog" (poi dog) of the Society and Sandwich islands and its relative, the "New Zealand dog." He puts the poi dog into three classifications, namely, *Canis feri*, *Canis terrarius*, and *Canis Pacificus*, Nob. The

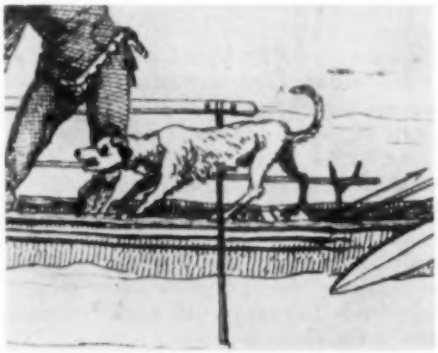

FIG. 20. Detail of Papuan native dog in Figure 19.

New Zealand dog is in the first two classifications and may be in the third, but Smith is not clear upon this point. A search of zoological indices has not revealed "*C. Pacificus,* Nob." among new species, or any productive clue either to the identity of the natural scientist whose name is abbreviated as "Nob." or to the location of his original description. The classification continues to be cited, however, probably secondarily from Smith (Davis, 1949: 12).

Under *Canes feri,* Smith lists wolf dogs, watch dogs, greyhounds, hounds, cur dogs (terrier, Lapland cur, pariah dog, poi dog, New Zealand dog, Patagonian dog, Tierra del Fuego dog), and mastiffs. His second classification "*Canis terrarius—Canes Domesticii*" he describes as being below middle size in height and having a round head, pointed muzzle, erect ears, large and prominent eyes, and the characteristics of being sagacious, noisy, and watchful, and separable into three distinct species. He includes here terriers, pariahs, poi dogs, New Zealand dogs, and the Patagonian and Fuegian dogs. His third classification of the poi dog is *Canis Pacificus.* Nob. His two classifications of the dingo, by the way, are *Chaon Australiae* and *Chryseus Australiae.*

Smith is vague about his sources. He mentions J. R. Forster as describing the New Zealand dog as short and with a tufted tail, a very large head, small eyes, and pointed ears. George Forster, it will be recalled, writes of the Society islanders feeding pigs breadfruit paste (poe) called *mahei.* Smith refers to "Frederick Bennet" (*sic*) in connection with the poi dog but he has obviously drawn on more than Bennett's book, as we shall see.

Some of Smith's data may come from King's account, which likens the Hawaiian dog to the turnspit. Both Crozet and Captain Cook compare the New Zealand dogs with fox-dogs. Reverend William Ellis (1853, IV: 347) compares Hawaiian and Tahitian dogs with terriers. The Hawaiian dogs that Ellis saw in 1819 were "of rather a small size, and something like a terrier." Tahitian dogs were "usually of a small or middle size and appear a kind of terrier breed, but were by no means ferocious; and excepting their shape and habits, they have few of the characteristics of the English dog. This probably arises from their different food. . . ." Smith's description of the dog's tail as being straight or slightly curled is absent in earlier accounts. I cannot locate his source, but Hawaiian petroglyphs portray dogs with slightly curved tails (see Fig. 22). Another possible source Smith might have been familiar with is George Dixon's description (1789: 266) in September, 1787, of the Hawaiian dogs as appearing "to be of the cur kind, dull and heavy; they have sharp pointed ears projecting toward the nose." (See Figs. 13, 14, 15.)

F. D. Bennett, one of Smith's sources, was a fellow of the Royal College of Surgeons, who between 1833 and 1936 travelled around the world to study sperm whales. Although he really says very little about the dog from his own observations, he is one of the few scientists writing about Pacific dogs who has actually seen one, dead or alive, mixed or unmixed in breed. After mentioning the pig, he writes (1840, I: 86), "The aboriginal dog has also merged into a mongrel breed. The Tahitians formerly considered a dog, fed on vegetable food, a delicate dish; and although the impairment of the purity of the breed, and the prejudices of Europeans, have done much to abolish this state, it is still not unfrequently indulged." Although he gives no references, a phrase like "delicate dish" is reminiscent of the journals of the Cook expeditions. In a later description his comparing of dog meat with lamb and calling it a dish not to be despised recalls Cook's famous description of how to cook a Tahitian dog for the table. Later culinary adventurers often echo Cook's evaluation of the meat although Vancouver (1798, III: 61) varies it, after a meal with King Kamehameha I, by comparing the meat with mutton.

Bennett's list of the physical traits of the Hawaiian dog recalls, at least in part, King's description. Bennett writes (1840, I: 246):

> The indigenous and exotic quadrupeds resemble those at the Society group. The aboriginal, or poe dog, characterised by its small size, brown colour, foxy head, long back, crooked or bandy fore-legs, and sluggish disposition, is now a rare, and will probably be soon an extinct species—lost amidst a mongrel race of dogs partaking of every foreign variety. All classes of canines are favourites with the natives, who never kill them wantonly or treat them cruelly. They subsist,

like their owners, chiefly on vegetables. The aboriginal food is still considered a delicate food, even by the chiefs highest in rank and most civilised in their habits. Europeans who have sufficiently overcome their prejudice to indulge in this native luxury, assured me that the flesh of the poe dog, cooked in the primitive manner, bears close resemblance to lamb, and is consequently a dish that few who have tasted would despise.

In Honolulu, October, 1835, Bennett writes (1840, I: 216), "A hut, called by foreigners the 'native hotel,' has also been opened as an eating house for the same class of people; and here, it is not uncommon to see a skinned dog suspended invitingly at the door, to denote what dainties may be had within, in the same manner as a turtle or a haunch of venison is occasionally exhibited at *restaurateur* establishments in London."

Later while visiting Timor, Bennett writes (1840, II: 109) that the "swine, dogs, and domestic fowls found on all the Polynesian groups, and apparently coeval with man in their existence on those lands, betray much of an Asiatic origin."

L. J. Fitzinger, in his summary of the binomial classifications of the domesticated dogs of the world, includes Polynesian native dogs (1867: 382, 400–401, 499, 520, 528–529, 817). He distinguishes seven basic types of dogs in the world and puts the Polynesian dogs, which he divides into two breeds, with the pariah dog (*Canis domesticus indicus*). The two breeds, he states, derive through acclimatization in Polynesia of the Asiatic large pariah dog that ancestors of the Polynesians brought with them into the Pacific. This recalls the fact that in 1827 Peter Dillon (1829, I: 254) writes that in New Zealand "They have a breed of dogs peculiar to the island, and much resembling the Pariah dog of India and which is considered as furnishing a most delicate dish." Because Fitzinger (1867: 528) regards the pariah and the pomeranian as derived from the ancestral type of house dog and as sharing many resemblances, it is of interest that in 1793, more than 20 years after Cook had brought native dogs to Tongatabu, Labillardière (1800: 128) says that the dog there "is commonly of a fallow color, small and pretty near resembling the Pomeranian dog." Others, in later times, also liken the native dogs, especially in New Zealand, to pariah dogs and pomeranians (Thomson, 1922).

The following is Fitzinger's material relating to the Polynesian dog.

1. *Canis domesticus, indicus Novae-Zeelandiae.* Included are the New Zealand dog described by George Forster (1778, I: 165); *Canis familiaris villaticus, novae Zeelandiae* of Walther (1817: 23); *Canis otahitensis* of Reichenbach (1836: 46, figs. 573–575); *Canis familiaris orthotus* of Reichenbach ("Naturg. Raubth.," 141, figs. 573–575); the New Zealand dog of Smith (1845: 211, 296); *Canis australis* of Youatt (1846: 32–43; cited is only a German edition of Youatt, p. 26); and *Canis familiaris otahitensis* of Giebel (1859: 844).

Fitzinger (1867: 529) considers that this New Zealand dog, which he believes has obvious characteristics of the large pariah dog (*Canis domesticus, indicus*), undoubtedly is a variation of it. The slight differences in its bodily traits inevitably arose, he suggests, from its acclimatization in New Zealand on being brought from the Asiatic mainland and the East Indies. The differences are the smaller size, the blunter muzzle, and the more elongated body of the New Zealand dog as compared with the pariah dog. The color is mostly a solid rusty-red, black, or white, but also commonly spotted, the white ground color being covered with irregular black or rusty-red spots of various sizes, particularly on the cheeks around the eyes and ears.

2. *Canis domesticus, indicus taitiensis,* the Tahitian dog, found in the Hawaiian and Society islands, has only minor differences from the New Zealand dog, its closest relatives. Like it, Fitzinger states (1867: 529), acclimatization in Polynesia has led to slight variations from the ancestral large pariah dog. Of a smaller size than the New Zealand dog, the Tahitian dog resembles the crooked-legged dachshund (*C. vertagus*), Fitzinger continues, in its somewhat more elongated body and shorter legs, of which the forelegs are not completely straight but seem somewhat crooked. The color is solidly brownish or rusty-gold. This, to Fitzinger, is the dog described by George Forster for the Society Islands (1778, I: 286); *Canis familiaris villaticus, meridionalis* of Walther (1817: 23); Reichenbach's

(1836: 46) *Canis otahitensis;* his ("Naturg. Raubth.": 141) *Canis familiaris orthotus otahitensis; Canis Pacificus,* the "Poe dog" of the Pacific islands, of Smith (1845: 210, 296); and *Canis familiaris otahitensis* of Giebel (1859: 844).

THE POLYNESIAN DOGS AND THOSE OF MELANESIA AND NEW GUINEA

That Fitzinger (1867: 817) also has an extensive synonymy for two other Oceanic species besides the two breeds he distinguishes in Polynesia is a further reminder of the ramifications of the problems connected with the history of Polynesian dogs. Fitzinger classifies the dingo as *Canis Novae-Hollandiae* and the dog of New Guinea and New Ireland as *Canis Novae-Hiberniae.* The latter classification combines the New Guinea dogs described by Captain Forrest with those of New Ireland described by R. P. Lesson and P. Garnot. Fitzinger refers to both the dingo and the Melanesian dog as being half-tamed.

Pennant, who, it will be recalled, was familiar with Forrest's reference to the fox-looking dogs called Naf, considers New Guinea as a dispersal area of dogs—and much else—to Polynesia and perhaps to Australia. Lesson and Garnot (Duperrey, 1826, I: 123, 127, 132), who visited the same coastal area of Daru in Papua, New Guinea, report the same native name as Nafe. They describe the dogs of Australia, Papua, and the Melanesian islands of New Ireland, Buka, and Bougainville, as being so much alike as to belong perhaps to the same species. The New Ireland dog, which the natives call *poull* and eat, is small-bodied, with short hair that is either tawny or black, and with a pointed muzzle and short, erect ears. Courageous and carnivorous, it hunts on the reefs for its meal of fish and crabs. Writing specifically of the Australian dog, the scientists liken it to the *chien de berger* (see Fig. 17) as Forster did the New Zealand dog. Another account (Laurillard, 1849, III: 545), perhaps quoting from Lesson's later statements which I have not seen, varies slightly; for instance, the New Ireland dog is said to have spindly legs and to be smaller than the New Holland dog.

From other references to Melanesia and New Guinea dogs I shall select two or three provocative of comparisons with the Polynesian dogs, and hope to lure a zoologist to interpret the findings of other zoologists for which my one semester on the zoology of a worm and a frog did not prepare me.

Small black and white dogs are reported from the interior of British New Guinea and from Goodenough Island. A. S. Meek in 1896 found them "fairly numerous" in the latter island where, it was thought, no white man had been. Later, Sir Hubert Murray, governor of British New Guinea from 1907 to 1940, sent to Australia specimens of black and white dogs found around Mt. Scratchley. Presumably these are the same specimens that De Vis classified in 1911 as *Canis familiaris* Linnaeus (quoted from Le Soeuf and Burrell, 1923: 92, 93), and that Wood-Jones in 1929, without mentioning De Vis, studied as part of his series of projected papers comparing the domestic animals, particularly the dog, of Pacific islanders in the hope of shedding some light on the racial origins and racial movements of the people whom the animals accompanied. His study of the dingo has been mentioned; the Hawaiian study will be referred to later. Apparently, Wood-Jones never compared the measurements of dog crania from the three areas or continued with his project.

According to De Vis, the dog is black and white, with black predominant. The rather bushy tail reaches the middle of the lower leg. The dew-claw is absent. The neck is thick and short, the head comparatively small, and the muzzle deep and narrow. The eyes are slightly oblique, and the ears short and erect. The short hair is "closely adpressed, without under fur, longer on neck, forming ruff between shoulder and ear." Head and body measure 650 mm.; the height at the shoulder is 290 mm.

Wood-Jones (1929: 331), who gives a series of measurements, with two sketches, of the two crania (Nos. 3751 and 4083, Queensland Museum), concludes that the skulls are those of small dogs "of the terrier type, with fairly elongated sharp noses and well developed muscular crests and ridges." This Papuan breed, except for its "relatively large upper carnassial tooth typical of primitive canine breeds," dif-

fers "widely in its characters from the dogs of certain other Pacific islands" that are not named. The peculiarities are that the palate has a backward prolongation behind the last molar tooth; the supraorbital processes are pointed in form (the dingo's were "swollen," and appeared convex on the upper surface), "flat to concave on the upper surface, and singularly vulpine in character," and the sagittal crest "is formed by a coalescence of the temporal ridges in the region of the coronary suture in both specimens, and . . . is extremely prominent in its caudal extremity where it joins the well marked nuchal crest." Wood-Jones (1929: 331) quotes, perhaps from a letter from the museum director, a more detailed description of the colors of two skins that have apparently been preserved; one is black and white, with black dominant; the other is "Ridgway's russet. . . ."

Wood-Jones, it will be noted, finds something foxlike about this breed. This suggests that those early Europeans who called the native dogs of the Pacific "foxlike" were not influenced to do so by theories of the day that some breeds of dogs were derived from a fox ancestor.

The trail of the dog goes, of course, farther west than New Guinea. Interestingly, some writers on Indonesian dogs note oblique eyes among them or find traits that recall to them the dingo. Northward in Micronesia, where the dog was spottily distributed at the time of European discovery, there are many problems that also show that to learn more about the Polynesian dogs the entire South Pacific must be studied. In this paper I shall ignore Micronesia, however, and turn to the Hawaiian dog.

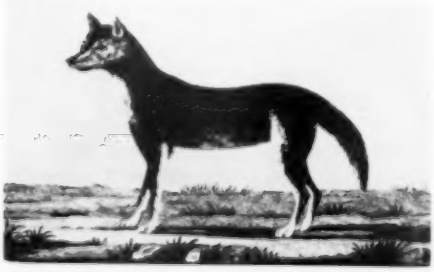

FIG. 21. An Australian dingo (Phillip, 1789 : pl. 45).

TWENTIETH-CENTURY STUDIES OF THE HAWAIIAN DOG

Few attempts to classify the Hawaiian dog have been made in the present century. Two zoological surveys (Sharp, 1913, I: 465; Bryan, 1915: 295) venture no description or classification. S. W. Tinker (1938: 84–87) gives no references but labels the dog *Canis domesticus hawaiiensis*. Like Bryan, he mentions the presence of color types distinguished by Hawaiians and probably follows David Malo (1951: 37) and references to dogs in native traditions and in Hawaiian-language newspapers. Tinker describes the colors as ranging from white through all of the yellowish and reddish shades to brown, with the lighter shades seemingly most numerous. The rest of Tinker's account seems to be derived from King and Wood-Jones. D. H. Johnson (1944: 334, 335), who does not describe but lists both the New Zealand and the Hawaiian dog as *Canis familiaris* Linnaeus, merely remarks that it was a domestic dog of Asiatic origin which Polynesians had purposely carried with them on their migrations.

Neither of the two major modern scientific studies of the physical traits of the Hawaiian dog gives any classification. However, they will be summarized because they point in the direction of our only hope now of learning more about the native dog.

Wood-Jones (1931) describes two crania of dogs believed to be possibly of the pre-European type, as they were obtained from Hawaiian archeological sites. Examination of the skulls reveals that although the cranial characteristics of the Hawaiian dog had greatly altered through a soft vegetable diet, the teeth had retained their primitive trait of large size. The relatively great length of the upper carnassial tooth is particularly noteworthy. This primitive trait recalls the New Guinea and Australian breeds. However, the Hawaiian canine skulls vary in many details from these western forms.

Wood-Jones writes, "The most conspicuous feature of the skull of the Hawaiian dog is the rounded and smooth contour of all parts of the cranium. The temporal lines are hardly visible; they are separated by an interval of nearly 30 mm. at the vertex, and the skull is therefore entirely devoid of a sagittal crest. The supra-

orbital processes are roundly convex and blunt. The muzzle is short and rounded, and the palate short and broad. The posterior margin of the palate is in line with the hinder portion of the last molar tooth." He gives in detail the cranial measurements of the two specimens. One, that of a young animal found in Nuololo Valley, Kauai, as a separate burial bundle in the general wrappings of a child, is in the Bishop Museum. Unstated is the present location of the second specimen, that of an adult dog from a burial cave at Nuololo Flat, Kauai. Both specimens were found wrapped in tapa.

Without citing a source, Wood-Jones also describes the appearance of the native Hawaiian dog. Probably he used Fitzinger, Ellis, King, and local Hawaiian informants for some of his account. The statement that one foreleg was commonly more bent than the other has not previously been recorded. Wood-Jones states:

> In general, however, we know that it was a long-bodied, short-legged dog of the short-haired terrier type. In general build it has been likened to the dachshund but, unlike this breed, its large ears were held erect. The tail was carried with an upward curve and the coat color appears to have been varied; but white and pale yellow are said to have been predominant. The fore limbs are described as being bandy, and it is said that very commonly one leg was markedly more bent than the other. Although the pure breed has ceased to exist in the islands of the Hawaiian group, there is abundant evidence of the persistence of its blood in the large number of long-bodied, short bandy-legged mongrels to be met with even around Honolulu. At times it would seem that the combination of characters, said by the old Hawaiians to be typical of the poi dog, is very faithfully reproduced in dogs of extremely mixed ancestry. It is by no means uncommon in Hawaiian villages to meet with these long, low dogs that have an unfamiliar appearance in consequence of their large erect ears.

The most recent study of the Hawaiian native dog, an examination of its teeth for caries, has been done by Dr. Arthur Svihla (1957), who is extending the study to visit museums in Polynesia to examine teeth thought to be derived from native dogs. The Hawaiian canine skulls and lower jaws that he examined came from archeological sites on Oahu and Hawaii. Skeletons of dogs are especially numerous in caves of refuge because women and children who sheltered in them took live pigs and dogs to provide part of their food. Dr. Svihla, who finds dental caries markedly prevalent in the teeth of these dogs, attributes the decay to the diet which was heavily weighted with starches and sugars. Food tabus, especially as relates to meat, had affected the women and the commoners who, although the caretakers of the pigs and dogs, were forbidden to eat them and fed them the staple vegetables of their own diet. Teeth of modern dog skulls in Bishop Museum have no caries, Dr. Svihla reports. He suggests that it is probably because the Hawaiian diet changed to include more protein after European contact and the abandonment of tabus. The diet of the dogs improved with that of their caretakers.

These studies by Wood-Jones and Svihla provide some support for the theories of the Forsters, King, Ellis, and others that the predominantly vegetable diet of the Polynesian dogs had caused some of the peculiarities of their appearance and behavior.

CONCLUSION

This paper has surveyed the literature on the taxonomy of the Polynesian native dogs. The source material of taxonomists has been derived, often at second- and third-hand, from impressionistic descriptions by members of the expeditions of Captain Cook and other eighteenth-century explorers, none of whom give a single measurement or apparently preserved a specimen for scientific study. Information from later centuries is open to doubt because interbreeding between native and introduced dogs began with the arrival of the first European ships with pet dogs aboard. No numerical data exist on the native dogs of the Society Islands and the Tuamotus. No measurements existed of Hawaiian native dogs until the twentieth century when, using archeological material presumed to be of pre-European age, Wood-Jones studied two crania and Svihla examined teeth for caries. No measurements were made on New Zealand dogs until the nineteenth century, by which time the identification of any living dogs as

representative of the pre-European variety was much disputed.

Four Polynesian archipelagoes—Hawaii, New Zealand, Society, and Tuamotus—had living native dogs at the time of European discovery. Archeological evidence from the Marquesas now shows that dogs had become extinct or very rare there by 1595, when Europeans are first known to have discovered the islands. Some islands, like Tonga, that had no dogs but recognized them, may also have had them once or heard about them from other islands.

Dogs are thought to have been brought to Polynesia by the first human discoverers and settlers of the area. The frequency with which early European artists showed dogs in canoes suggests that the dogs perhaps always made sure that they were not abandoned. Wood-Jones hoped through studying Pacific native dogs to learn something of their owners' migrations. One natural scientist favored New Guinea as a dispersal center of people and culture. Another who compared dogs of New Guinea and neighboring islands of Melanesia, not all of which had dogs, likened them to the Australian dingo. The dingo has also been compared with dogs to the westward in Indonesia and to the eastward in New Zealand. However, the fact that dogs of unknown breeds were introduced into New Zealand from Australia in the nineteenth century makes the question of dingo and Maori dog relationship difficult to answer without scientific measurements of ancient native forms. Although Polynesian dogs have been likened to many different mongrels and curs of the Old World, some natural scientists consider their closest kin to be among Asiatic pariah dogs. The place of Micronesian dogs in the Pacific scene remains to be considered.

The taxonomists, from their limited primary source material, feel that at least two breeds, which they do not define clearly, existed in Polynesia at the time of discovery by Europeans. The most distinctive of the superficial traits (the only kind described) was perhaps the length or quality of the hair. Some Maori and Tuamotuan dogs were especially valued for the long silky texture of their hair. Very early the natural scientists remarked on the possibility of adaptations resulting from the owners' care and exploitation of their animals for food or fur. Recent studies of native canine teeth show that the predominantly vegetable diet of pre-European Hawaiian dogs favored the development of caries. Latter-day concepts, like that of genetic drift, have not been considered in connection with the possible emergence of local varieties as the result of line breeding from perhaps a single pair isolated on an island. Study of Hawaiian canine skulls shows the persistence of the long upper carnassial tooth, a primitive trait, but the emergence of noticeable deviations in some characteristics of the skull as compared with Papuan and Australian forms.

To state the goals of those studying Pacific dogs makes these goals more specific than they are actually stated in most studies, but they underly the research of the past and remain for that of the future. The purposes have been: (1) to trace through the spread of domestic animals the wanderings of their owners as they dis-

FIG. 22. Petroglyphs that include dogs, Nuuanu Valley, Honolulu, Hawaii (Bishop Museum Negative 6809).

covered and settled the island world; (2) to classify Polynesian breeds of dogs in relationship to other dogs of the Pacific and of the world, and to determine the closest kin of the island dogs among the breeds elsewhere; and (3) to determine how the peculiarities of the Polynesian and other Pacific dogs originated through artificial and natural selection, mutation, genetic drift, and adaptations resulting from domestication and human use and care.

Now, more than 350 years after the first known European contact with Polynesia, progress toward these goals and toward learning more about *Canis familiaris* Linnaeus of pre-European Polynesia must depend upon studying museum skeletal remains and artifacts made of dog bones, teeth, and hair, and recent archaeological finds of remains of dogs that are datable by radiocarbon analysis as pre-European in age. Research like that of Wood-Jones and Svihla gives hope that even at this late date something may be learned of the characteristic of the Polynesian dogs and of the origin of local variations.

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Revision of the Genus *Pandanus* Stickman
Part 1. Key to the Sections

HAROLD ST. JOHN[1]

FOR THIRTY YEARS the writer has lived and has made plant collections on the tropical Pacific islands, the home of a great part of the genus *Pandanus* (Pandanaceae). His gatherings of the genus are numerous.

In 1955 and 1957 grants were received from the National Science Foundation of the United States, to make possible extensive exploration for this genus in the Pacific, for the employment of an assistant, and for research investigations. Most of the species are trees with elongate, saw-toothed blades, and large, fleshy fruits that are difficult to dry. Many of them have unpleasantly spiny trunks, branches, and even roots. Consequently, the collecting of specimens is difficult or hazardous, and the drying of them is a long and burdensome process. But few of the botanical explorers in the Pacific have had the interest or the endurance to make extensive collections of *Pandanus*. Most of the others, when collecting their first specimen, have been lacerated by the saw-like leaves or wounded by the spines of the trunk. They have then uttered an oath and sworn never to collect another *Pandanus*. As a result the *Pandanus* population has been well sampled in only a few areas.

Outstanding among previous explorers was Prof. Ryozo Kanehira of Kyushu University, who revealed much of the wealth of *Pandanus* in the Caroline Is., Marshall Is., and New Guinea.

Since 1955 the writer or his assistant, Benjamin C. Stone, have made lone explorations for *Pandanus* in the Ryukyu Is., Marianas Is., Caroline Is., Marshall Is., New Guinea, Bismarck Arch., Solomon Is., the New Hebrides, and the Hawaiian Is. In almost every one of these islands or archipelagos were discovered from two to five times as many kinds of *Pandanus* plants as were known there from earlier explorations.

The writer envisions that his published studies will form a revision of the genus, or at least of its species occurring in the Pacific. As small portions of it are finished, they will be published as numbered parts, with a consecutive paging, under one general title. In this way the finished parts can be made available early.

Many of the present sections of the genus are those groups recognized as genera by Gaudichaud. When only a few species were known, many of these groups seemed truly good genera. With the increase in the number of species to nearly 600, the "generic" distinctions have diminished or vanished. Hence, the writer concurs with the judgement of nearly all recent investigators that *Pandanus* is one very large genus that contains numerous well-marked sections. There is nothing to be gained by classing them all as subgenera, so the writer follows Warburg (1900) in dividing the genus into sections. More sections have been added recently, especially by E. G. R. Pichi-Sermolli (1951) in his study of the species of Madagascar.

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KEY TO THE SECTIONS

A. Drupes all or mostly 1-celled (subgenus *Lophostigma*),
  B. Stigmas broader than long, flat,
    C. Stigmas flush, horseshoe-shaped, glabrous; drupes ellipsoid; syncarps solitary, spicate, or racemose; stamens umbellate at apex of column ..... *Microstigma*
    C. Stigmas raised; drupes cuneiform or fusiform,
      D. Stigmas as broad as or broader than apex of drupe,
        E. Stigmas oblate capitate, emarginate, as broad as the narrow apex of the fusiform drupe, in anthesis hirsute; heads single; staminate flowers unknown ..... *Pulvinistigma*
        E. Stigmas discoid suborbicular, entire or lobed, broader than the cuneiform drupes, glabrous, imbricate and concealing the drupes; staminate flowers unknown ..... *Asterostigma*
      D. Stigmas narrower than apex of drupe, lunate, lateral under a horizontal, coriaceous, entire or lobed visor borne asymmetrically on the apical region of the drupe but not marginal; staminate flowers unknown ..... *Maysops*
  B. Stigmas longer than broad or orbicular,
    F. Stigma 1 (rarely 2), setiform, at maturity deciduous from the pileus; staminate flowers unknown ..... *Rykiella*
    F. Stigmas broader than setiform, persistent,
      G. Stigmas erect, crested and laterally expanded; staminate flowers unknown ..... *Cristata*
      G. Stigmas not crested,
        H. Style subulate, apical, erect or ascending, bearing a distal stigma; stamens attached to axis, the column lacking ..... *Acrostigma*
        H. Stigmas broader than subulate,
          I. Stigma on lateral edge of pileus, and horizontal, toothlike, entire; stamens crowded on conical apex of column ..... *Lophostigma*
          I. Stigma terminal,
            J. Stigma a flat flap, entire or lobed, often orbicular or reniform, ascending or spreading; stamens umbellate on adaxial side of column apex ..... *Microstigma*
            J. Styles 1 (–2), toothlike to broad subulate, hornlike, cartilaginous, erect or spreading, bearing a proximal stigma; stamens fascicled at apex of column ..... *Rykia*

A. Drupes or phalanges all or mostly several-celled (subgenus *Pandanus*),
  K. Marginal carpels the smaller, acerose toothlike, mostly sterile; phalanges 5–10-celled; stamens few, on dichotomous apex of column ..... *Stephanostigma*
  K. Marginal carpels not toothlike and sterile,
    L. Stigmas elongate, acerose,
      M. Stigmas acerose, mostly forked; stamens umbellate on capitate apex of column ..... *Multispina*
      M. Stigmas of simple, acerose spines; staminal column bifid with digitate filaments that are simple or 2- 3-forked ..... *Acanthostyla*
    L. Stigmas not acerose elongate,
      N. Stigmas apical and oblique or erect (or a small percentage of them horizontal),
        O. Carpels in 1 transverse line or in several parallel such lines; stamens borne under a peltate apex of the column, or in several racemes with subtending bracts ..... *Hombronia*
        O. Carpels in circular, centripetal, or irregular arrangement, not a linear one,

P. Other stigmas all facing a single marginal one or facing the marginal ones along one side; staminate flowers unknown ..... *Lateriobtutus*
P. Stigmas centripetal; stamens subfasciculate or racemose ..... *Pandanus*
N. Stigmas flush, not ascending or oblique,
Q. Stigmas apical,
R. Phalange with a fibrous septum between the 2 cells; stigmas approximate; stamens umbellate on the capitate apex of the column, and with abortive gynoecium ..... *Martillidendron*
R. Phalange of several (or 1) cells, each with a bony endocarp,
S. Phalange not lobed, the summit broad convex,
T. Stigmas 2–7, all (or all but one central one) centripetal, and on the margin of an apical ring or polygon; stamens unknown ..... *Dauphinensia*
T. Stigmas 1–9, centripetal, approximate in central area of broad, low convex apex; staminate column fasciate, bearing short terminal, free filaments, or filaments united 1/6–½ way in groups ..... *Vinsonia*
S. Phalange apex lobed,
U. Phalange apex broad convex or narrow, shallowly lobed between the 2–9 stigmas ..... *Vinsonia*
U. Phalange much narrowed to truncate (or concave) apex where the numerous carpel tips are crowded,
V. Carpel apices low conic or low pyramidal, crowded; staminal column ± diffusely branched into short filaments shorter than the anthers ..... *Mammillarisia*
V. Carpel apices narrow deltoid or slender conic, the outer ones inflexed and very asymmetric; stamens unknown ..... *Australibrassia*
Q. Stigmas markedly subapical,
W. Stigma on distal surface of carpel tip; staminate flowers unknown ..... *Coronata*
W. Stigma on proximal surface of carpel tip; staminate flowers unknown ..... *Intraobtutus*

SYNOPSIS OF SECTIONS

SUBGENUS *Lophostigma*, subgen. nov.

Carpellae drupas distinctas formant. Carpels distinct, in fruit forming drupes.

HOLOTYPUS: section *Lophostigma* (Brongn.) Warb., in Engler's Pflanzenreich IV, fam. 9: 71, 1900.

There has been effectively published the subgeneric name *Acrostigma* by Martelli, Soc. Tosc. Sci. Nat., Atti, Proc. Verb. 42: 56, 1933. However, this name was printed without a description or a reference to one. This taxon "sottogenere" was not formally accepted by its author, Martelli, and he used it indiscriminately with "sezione," but the latter taxon, the section, was the one he actually accepted.

The sections in this subgenus follow in alphabetical order:

Acrostigma Kurz, Jour. Bot. Brit. and For. 5: 100, 1867; As. Soc. Bengal, Jour. 38(2): 146, 1869. Lectotype: *P. affinis* Kurz, Jour. Bot. Brit. and For. 5: 101, 1867. The section contains 51 species, and it occurs in: western Africa (1 species), India (15), Ceylon (3), Burma (1), Malaya (15), Thailand (2), Indochina (3), Philippines (5), Indonesia (23), New Guinea (14), Bismarck Arch. (1), Australia (2), and Fiji (1).

Asterostigma Martelli, Webbia 4(2): 427, 1914. Lectotype: *P. discostigma* Martelli, Webbia 4(2): 427, pl. 39, figs. 12–15, 1914, Borneo. The one other species, *P. stelliger* Ridl., is from Malaya.

Cristata Martelli, Philipp. Jour. Sci. Bot. 3C: 70, 1908. Type: *P. Cumingianus* Martelli, from Negros, P. I., the only species.

Foullioya (Balf. f.) Warb., emend. Pic.-Ser., Engler's Pflanzenreich IV, 9: 44, 73–74, 1900

(as *Fouilloya*); and Inst. Sci. Madagascar, Mém. sér. B, 3(1): 97–100, 1951. The genus *Foullioya* Gaud., Bot. Voy. La Bonite, Atlas, pl. 26, figs. 1–9, 21–24, (1843) [= 1841] was without description and contained two species, hence was invalid. The earlier spellings of the generic and sectional name were all *Fouilloya*, except for that by Kurz in 1869, and Pichi-Sermolli (1951: 100), who, after biographical investigation, corrected the spelling to *Foullioya*. He found no man named Fouilloy, but did learn of an associate of Gaudichaud's, the surgeon Foullioy, who served on a French naval expedition to Madagascar. From these facts, the correction in spelling by Pichi-Sermolli seems reasonable and permissible. The section contains five or six species from Madagascar.

Lophostigma (Brongn.) Warb., in Engler's Pflanzenreich IV, 9: 44, 71, 1900; genus *Bryantia*, section *Lophostigma* Brongn., Ann. Sci. Nat. Bot. VI, 1: 287, 1875. Lectotype: *Bryantia viscida* Brongn. = *Pandanus viscidus* (Brongn.) Solms, of New Caledonia. The section contains five species: New Caledonia (4), and Fiji (1).

Maysops, sect. nov. Drupis 1-carpellatis fusiformibus vel suboblongis, stigmatibus lunatis sub margine petaso horizontale coriaceo integro vel lobato in apice sed asymmetrico, syncarpiis cylindraceis obtusis in bracteis naviculatis coloratis multis toto amplectis, drupis luteis aurantiacis vel subroseis eis apicalibus praematuris.

Drupes one-celled, fusiform to somewhat oblong; stigmas lunate, lateral under a horizontal, coriaceous, entire or lobed visor borne asymmetrically on the apical region of the drupe but not lateral; syncarps cylindric, obtuse, completely enwrapped in many boat-shaped, colored bracts; drupes yellow, orange, or pink, ripening serially, the apical ones first and shedding in this order.

HOLOTYPUS: *P. Zea* St. John, from Queensland, Australia, described in this paper. Other species are: from the Solomon Is., *P. lamprocephalus;* from New Guinea, *P. cernuifolius, P. floribundus, P. Kivi, P. Krauelianus, P. microdontus, P. xanthocarpus;* from Amboina, *P. amboinensis;* and the writer has four more undescribed species from New Guinea. Other species that have the fruit and stigmatic characters, but have ovoid syncarps and lack the numerous sheathing, colored bracts, are: *P. Joskei* of Fiji; *P. aggregatus* and *P. Archboldianus* of New Guinea; and *P. Beccarii* of the Aru Is. These should probably be included in this section, though they lack some of the characters.

The sectional name is formed from the epithet *Mays* of *Zea Mays*, plus the Greek *ops*, appearance, because of the striking resemblance of the fruit of these species of *Pandanus* to an ear of corn or maize in its husk.

Microstigma Kurz, Jour. Bot. Brit. and For. 5: 104–105, 1867. Lectotype: *P. ceramicus* Rumph., Herb. Amb. 4: 149, pl. 79, 1743 = *P. conoideus* Lam., Encyc. Méth. Bot. 1: 372, 1783. *Bryantia* (Webb in Gaud.) Warb. in Engler's Pflanzenreich IV, 9: 68, 1900, was based on the genus *Bryantia* Webb in Gaud., Bot. Voy. La Bonite, Atlas, pl. 20, (1843) [= 1841], published without description, but monotypic and with a figure showing details. Its holotype was *B. butyrophora* Webb in Gaud. = *P. conoideus* Lam. (1783). Here, also reduced to synonymy, is the section *Sussea* Warb., Engler's Pflanzenreich IV, 9: 44, 62, 1900, since its alleged characters do not hold and no new dependable differences have been found. Lectotype: *Sussea conoidea* Gaud., Bot. Voy. La Bonite, Atlas, pl. 24, figs. 1–12, 1841 = *P. montanus* Bory. The enlarged section now contains 98 species, and occurs in: west Africa (8 species), east Africa (3), Madagascar (20), Seychelles (1), Reunion (1), Mauritius (4), India (1), Burma (1), Malaya (2), Philippines (19), Indonesia (10), New Guinea (17), Admiralty Is. (1), Bismarck Arch. (5), Solomon Is. (6), D'Entrecasteaux Is. (1), and the New Hebrides (1).

Pulvinistigma Martelli (as *Pulvistigma*) emend. Kanehira, Univ. Calif. Publ. Bot. 12 (12): 369–370, pl. 48, 1930. Type: *P. Durio* Martelli. The emendation by Kanehira was published in the Jap. Jour. Bot. 14: 435, 1938. He pointed out that as Martelli had said (1930: 370), "The stigmas are thickly covered with short hairs that form a small cushion." The name *Pulvistigma* would seem to have been derived from the Latin *pulvis*, but this means dust, and is inappropriate. On the other hand, the Latin word *pulvinus* means a cushion, and this exactly

describes the distinctive stigma of this species and section. Also in Martelli's diagnosis (p. 369) he used the words, "stigma . . . pulvinatum." Consequently, the emendation in spelling made by Kanehira seems permissible under the International Code of Botanical Nomenclature. The section contains two species from Borneo.

Rykia (De Vriese) Kurz, Jour. Bot. Brit. and For. 5: 101–104, 1867 (as *Ryckia*); Asiat. Soc. Bengal, Jour. 38(2): 147, 1869. Genus *Rykia* De Vriese, Akad. Amsterdam, Verh. 2: 203, 1854, and in Hooker's Kew Jour. 6: 268, 1854. The alteration to *Ryckia* De Vriese emend. Balf. f., Linn. Soc. Bot., Jour. 17: 35, 48, 1878, and Martelli, Webbia 4(1): 96, 1913, was unjustified. As De Vriese stated, the genus was named in honor of Vice-Admiral J. C. Ryk. The Index Kewensis has already judged this change in spelling by Balfour as a mistake. As a new synonym, is included the section *Epiphytici* Martelli, Webbia 4(1): 96, 1913; Soc. Bot. Ital., Bul. 304, 1904. Its single species, *P. epiphyticus* Martelli, from Borneo, has all the morphological characteristics of the section *Rykia*. The fact that it was found growing perched upon another plant, is considered of no taxonomic significance. Type: *P. furcatus* Roxb. The section contains 74 species and ranges from Madagascar to Australia: Madagascar (3 species), India (13), Ceylon (2), Burma (5), Thailand (3), Malaya (9), Indochina (9), China (2), Philippines (5), East Indies (22), New Guinea (1), and Australia (1).

Rykiella Pic.-Ser., Inst. Sci. Madagascar, Mém. B, 3: 155–158, 1951. Type: *P. macrophyllus* Martelli. This and the one other species occur in Madagascar.

SUBGENUS *Pandanus*

The use of the name *Pandanus* for this subgenus is required by the International Code of Botanical Nomenclature, since it contains the type section and the type species of the genus. It has long been known by the sectional name *Keura* (Forsk.) Kurz, Jour. Bot. Brit. and For. 5: 105, 1867. Type: section *Pandanus*. Drupes or phalanges all or nearly all several-celled.

Acanthostyla Martelli, Soc. Tosc. Sci. Nat., Atti, Proc. Verb. 42: 57, 1933; Inst. Sci. Madagascar, Mém. sér. B, 3: 11, 122–126, 1951. Type: *P. spinifer* Warb. The section contains 13 species of Madagascar.

Australibrassia, sect. nov. Phalangiis pluricarpellosis lobatis in apice valde angustatis, apicibus carpellorum anguste deltoideis vel conicis exterioribus inflexis et valde asymmetricis.

Phalanges much narrowed towards the apex, and there lobed between the numerous carpels; apices of the carpels narrowly deltoid or narrowly conic, the outer ones inflexed and very asymmetric.

HOLOTYPUS: *P. conicus* St. John. Its description follows. Also in this section is the new *P. cochleatus* St. John.

Coronata Martelli, Univ. Calif. Publ. Bot. 12(10): 359, 1930. Lectotype: *P. corallinus* Martelli, l. c. 395, pl. 45, fig. 10–12, 1930. The lectotype is from Tongatabu, Tonga. The other species, *P. Whitmeeanus* Martelli, is known from Tongatabu, and from Savaii, Samoa; and *P. esculentus* Martelli is from Luzon in the Philippines.

Dauphinensia, sect. nov. Carpellis (1)-pluribus, phalangiis integris in apice late convexis, stigmatibus omnibus (vel omnibus unico centrale excepto) in margine circulo vel polygono apicale.

Carpels (1)-several; phalanges entire and with the apex wide convex; stigmas all (or all except the single central one) on the margin of an apical circle or polygon.

HOLOTYPUS: *P. dauphinensis* Martelli in Martelli and Pichi-Sermolli, Inst. Sci. Madagascar, Mém., sér. B, 3(1): 38–40, fig. 5, 1951.

The section contains six species, including: from east Africa, *P. Stuhlmanni;* from the Seychelles, *P. Hornei;* from Madagascar, the type, and *P. concretus,* and *P. reflexus;* and from Guam, *P. Kafu.*

Hombronia (Gaud.) Warb., in Engler's Pflanzenreich IV, 9: 50, 1900; genus *Hombronia* Gaud., Bot. Voy. La Bonite, Atlas, t. 27, fig. 17, (1843) [= 1841]. The name was published by Gaudichaud without a description, but the genus was monotypic, and it was illustrated by a figure with details, so the name was valid. Type: *Hombronia edulis* Gaud., but the epithet is preoccupied in *Pandanus*, so the valid name is now *P. dubius* Spreng. The section contains 22 species, and it occurs from the Andaman Is. to

Samoa, as follows: Andaman Is. (1 species), Nicobar Is. (1), Malaya (1), Thailand (1), Philippines (2), Micronesia (3), Indonesia (1), New Guinea (8), Solomon Is. (2), New Caledonia (8), Isle of Pines (1), Loyalty Is. (2), New Hebrides (1), Australia (1), and Samoa (1).

Intraobtutus, sect. nov. Stigma centripetalum anguste ellipticum in latere proximo praerupto carpelli truncati affixa; carpellis plurimis et adnatis; plantis masculis incognitis.

Stigma centripetal, narrowly elliptic, borne on the proximal steep inner side of the truncate carpel apex; carpels 7, adnate 6/7 way; staminate plant unknown.

HOLOTYPUS: *Pandanus Parkinsonii* Martelli, Webbia 4(2): 417, t. 38, figs. 14–15, 1914. It occurs in the Bismarck Archipelago.

Lateriobtutus, sect. nov. Carpellis plurimis adnatis, stigmatibus carpellorum altrorum ad carpellam marginalem dirigitis vel ad lineam marginalem carpellorum dirigitis. Ei carpelli obtuti quam altros breviori. Arbori masculi incogniti.

Carpels several, adnate, the stigma of all the others facing one marginal or the line of several marginal ones at the proximal edge. The focal carpels shorter than the others. Staminate trees unknown.

HOLOTYPUS: *Pandanus biakensis* St. John, from Biak, Netherlands New Guinea, *H. St. John 26,142*, the description of which is appended at the end of this paper.

Mammillarisia, sect. nov. Phalangibus in apice angustatis truncatis lobatisque, apicibus carpellis pluribus approximatis depresse conicis vel pyramidatis, columnis staminalis diffuse ramosis filamentis brevibus ferrentibus.

Phalanges narrowed to a truncate apex, lobed; apices of the several carpels depressed conic or pyramidal, crowded; staminal columns diffusely branched, bearing short filaments.

HOLOTYPUS: *P. mammillaris* Martelli and Pic.-Ser., Inst. Sci. Madagascar, Mém., sér. B, 3(1): 47–51, fig. 6, a–e, 1951.

The section contains 26 species, including: from west Africa, *P. thomensis;* from Madagascar, *P. bipyramidatus, P. diffusus, P. Karaka, P. mammillaris, P. Pervilleanus, P. sambiranensis, P. saxatilis,* and *P. vanDamii;* from Reunion, *P. sylvestris;* from Mauritius, *P. drupaceus,* and *P. glaucocephalus;* from the Philippines, *P. acladus, P. biliranensis, P. camarinensis, P. luzonensis, P. Martellii, P. nobilis, P. panayensis, P. radicans, P. sibuyanensis, P. umbonatus,* and *P. urdatenensis;* from Palau, *P. Kanehirae;* from New Guinea, *P. Kaernbachii;* and from Australia, *P. Dammannii.*

Martillidendron Pic.-Ser., Inst. Sci. Madagascar, Mém., sér. B, 3(1): 20, 1951. Type: *P. androcephalanthus* Martelli. The section contains three species from Madagascar.

Multispina Fagerlind, Svensk Bot. Tidskr. 34: 112–113, 1940. Type: *P. multifurcatus* Fagerlind, from Java, the only species.

Pandanus. Type: *P. odoratissimus* L. f., of Ceylon. A synonym is the sectional name *Keura* (Forsk.) Kurz, Jour. Bot. Brit. and For. 5: 105, 1867; Asiat. Soc. Bengal, Jour. 38(2): 147–150, 1869; genus *Keura* Forsk., Fl. Aegypt.-Arab. 95, 122, 172, 1775, a familiar and long-used name. Since this section contains the type species of the genus, it is now mandatory to use the same name as the name of this section, in compliance with Article 22 of the 1956 International Code of Botanical Nomenclature. At first sight Solms seems to typify *Pandanus* in his monograph (Linnaea 42: 3, 1878): "Typus **P. Kurziani,**" but he does the same for several other species. Those are the ones which he chose to use to provide group names for groups of species (sections of other taxonomists). These are not valid subgeneric or sectional names, being binomials for collective species. On p. 77 he says: "P. odoratissimus L. fil. Nomen delendum omnes fere tunc descriptas Pandani species amplectens." Thus Solms rejected the holotype of the monotypic genus on the basis of confusions and misdeterminations by subsequent botanists. His rejection is unjustified.

At the moment, the section contains 169 species. A few of these occur in Africa and in the Indian Ocean: east Africa (6 species), Comore Is. (1), Madagascar (1), Mauritius (1), Seychelles (2), Ceylon (1), India (2), Nicobar Is. (2), Andaman Is. (1), but the great bulk of the species which remain (151) occur in the tropical Pacific, from its western shore

to Hawaii, the Marquesas Is., and the Tuamotu Archipelago.

Stephanostigma Pic.-Ser., Inst. Sci. Madagascar, Mém. sér. B, 3: 112–113, 1951. Type: *P. analamazaotrensis* Martelli, the only species, a native of Madagascar.

Vinsonia Warb., in Engler's Pflanzenreich IV, 9: 44, 54–62, 1900. The genus *Vinsonia* Gaud., Bot. Voy. La Bonite, Atlas, pl. 17, 19, 23, and 31, (1843) [= 1841], contained 10 species when published by Gaudichaud. There were no descriptions to accompany the illustrations of either the species or the genus, so his specific and generic names were all invalid, though some of them were later validated by subsequent authors. Lectotype: *Vinsonia sylvestris* Gaud., Bot. Voy. La Bonite, Atlas, t. 17, figs. 16–17, (1843) [= 1841]. It is a synonym of *P. Barklyi* Balf. f. in Baker, Fl. Mauritius 397, 1877, a native of Mauritius. This is chosen as lectotype for section *Vinsonia* because among the 10 species published by Gaudichaud in his genus *Vinsonia*, 3 were of this affinity and they made a large element of his concept. *V. sylvestris* was well figured by Gaudichaud and is known to be native of Mauritius. Brongniart found a holotype of it in the Paris herbarium. Since the genus *Vinsonia* Gaud. was published without a generic description, but contained 10 species, the genus and species were invalid. In the original publication of *P. Barklyi*, Baker listed *V. sylvestris* Gaud. as a synonym, so the relation to this valid name is definite. Of the remaining seven species in Gaudichaud's genus *Vinsonia*, one, *V. drupaceus*, was based on fragmentary and dubious material. *V. lucidus* is obscure. *V. palustris* belongs to section *Pandanus*. The four species, *V. elegans*, *V. humilis*, *V. Pervilleana*, and *V. purpurascens*, belong to the section with the phalange narrowed to a small apex on which the numerous stigmas are crowded. This group is here described as a new section. It could bear the name *Vinsonia*, but the writer prefers to typify it by *P. mammillaris* Martelli and Pic.-Ser., a modern and better documented species. To preserve usage he prefers to typify *Vinsonia* by choosing one of the three species, *V. sylvestris*, *V. stephanocarpa*, and *V. utilis*, which Gaudichaud figured, that represent the section with broad phalange, apex entire or shallowly lobed, and with the few stigmas remote. Of the three species, *V. sylvestris* Gaud. is chosen here as the lectotype for the section *Vinsonia*. The correct name for the lectotypic species is *Pandanus Barklyi* Balf. f. in Baker.

For the first time the section *Vinsonia* is here typified. At the same time it is restricted to 22 instead of 55 species. Of the remainder, *P. Eydouxia* is referred to the section *Pandanus*. Four species, and perhaps three doubtful ones, are assigned to the new section *Dauphinensia*. The distinctive characters of this were singled out by Martelli and Pichi-Sermolli, in Inst. Sci. Madagascar, Mém., sér. B, 3: 35–36, 1951, but they did not separate it as a section. Then, 26 species are grouped in the new section *Mammillarisia*. This is also a segregate from *Vinsonia* as formerly defined.

The generic name *Vinsonia* Gaud. was amended to *Vinçonia* by D'Alleizette, in his Explic. Descr. Pl. de l'Atlas 117, 1866. He failed to supply the missing descriptions, so his republication of the binomials is also invalid. His alteration of the generic name was orthographic, insignificant, and, under the rules of nomenclature, unnecessary. In concord with Vaughan and Wiehe (Linn. Soc. Bot., Jour. 55: 11, 1953) the section *Barklya* Warb. which was published in Engler's Pflanzenreich IV, 9: 44, 62, 1900, is reduced to synonymy. The 22 species of *Vinsonia* occur in: east Africa (2), Madagascar (1), Seychelles (1), Reunion (2), Rodriguez (1), Mauritius (11), Philippines (2), Kusaie (1), and Australia (1).

THE GENERIC NAME

Discussion is in order, concerning the publication of the generic name *Pandanus*, commonly attributed to Carolus Linnaeus the son (1781). It was first used as a generic name in 1743 by Rumphius in the fourth volume of his Herbarium Amboinense. There he described in great detail 11 species and illustrated 8 of them, each by a large, detailed drawing. He coined the generic name *Pandanus*, deriving it from the Malayan vernacular name of the trees, "pandan." Though no description of the genus was included, his treatment, the first under *Pandanus*, was by far the best for the next century. One

of Linnaeus' students, Olaf Stickman, was assigned the topic of the collation of the Herbarium Amboinense with the Species Plantarum of Linnaeus and the binomial system. All of the species of *Pandanus* published by Rumphius were given binomials in 1743, but Rumphius did not consistently follow the binomial system, and in any case, his book was pre-Linnaean, being previous to 1753 and so, by our International Code, illegitimate. Stickman in 1754 published his thesis under the title "Herbarium Amboinense." His thesis was concise and compact. In the left-hand column he quoted the names used by Rumphius, and in the corresponding right-hand column he entered the valid binomials that Linnaeus had published in 1753 for the same species, or for many others Stickman himself supplied the binomials. The genus *Pandanus* had not been given a name by Linnaeus the father, though Rheede van Draakestein had already illustrated some Indian species. In this part of his thesis Stickman left his right-hand column blank, thus failing to supply valid names for any of the species of *Pandanus*. He did, however, do something about the genus. Beside his listing of the first species of Rumphius, *Pandanus verus*, he referred to his own footnote (g). This is printed at the bottom of his page 17, "(g) Pandanus genus est nondum constitutum Monoeciae, Bromeliae forte affinis, fructu Ambrosiae." This refers to the extensive and well-illustrated treatment by Rumphius (1743), and to *Pandanus verus* Rumph., but Rumphius had not described his genus. Stickman wrote in his footnote (when translated): *Pandanus* is a genus not yet constituted, monoecious, with strong affinity to Bromelia, with a divine fruit. His sentence announces *Pandanus* as new, and gives three characters in his description. This satisfies the requirement that a new generic name must be accompanied by a description or a reference to one. Stickman failed to give legal names to any of the species but his publication of the genus is valid, as a genus may be published without species.

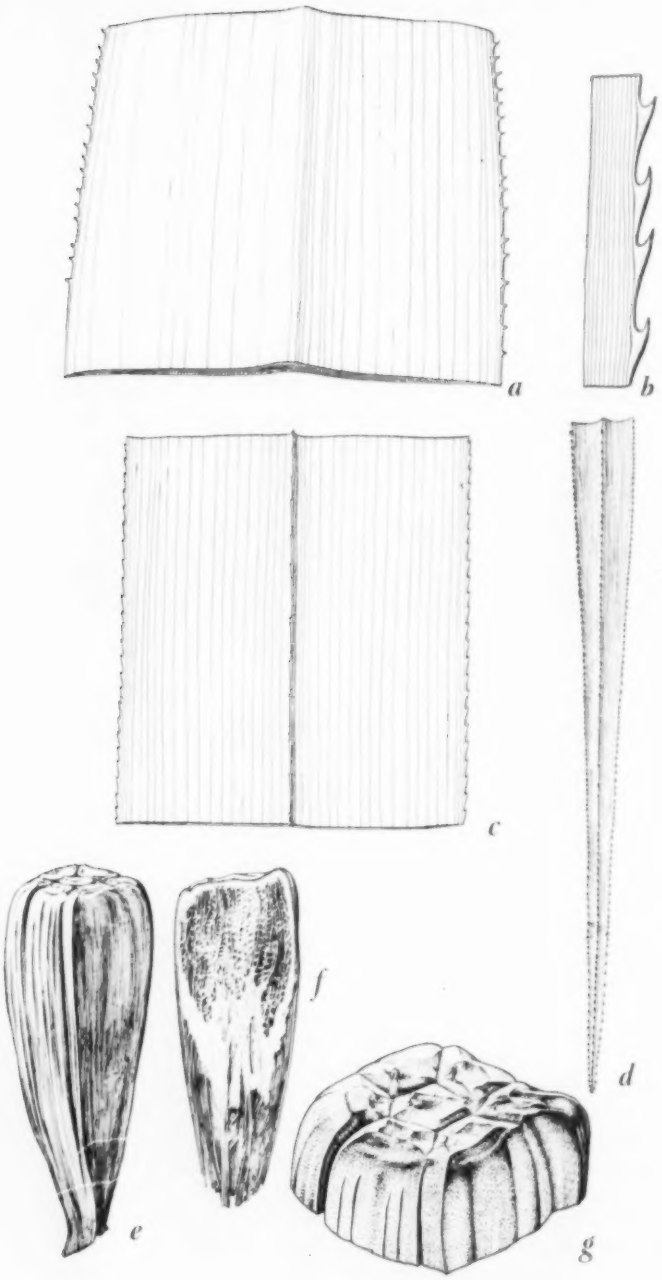
The names published by Stickman in his thesis of 1754 are commonly credited to Linnaeus, his professor. The title page of his publication includes the statement, "sub Praesidio D. D. Car. Linnaei," that is, written under the supervision of Prof. Linnaeus. It also states, "Proposuit Olavus Stickman, Smolandus, Upsaliae 1754," that is, this work is proposed by O. Stickman from Småland, at Upsala, in 1754. The thesis was printed, effectively published, and the author was Stickman. It also appeared in a second edition in the journal, Amoenitates Academicae, edited by Prof. Linnaeus, to reprint for wider circulation the best of the theses written by his students. Stickman's Herbarium Amboinense appears there in volume 4, printed in 1759. This second edition is essentially identical with the first, except that the title page material is a brief extract, and except for a few misprints, as, for instance, in the footnote (g), "...Monoecia...," the final *e* being missing. Stickman is given as the author of the article, and nowhere does Linnaeus claim it as his own. The articles in the several volumes of the journal are by numerous different authors, and the few written by Linnaeus himself bear his name as author. The name of Linnaeus is on the title page of the volume, but that means merely that he was the editor of the volume, not the author of all the articles written by his students and reprinted in this journal series.

SECTION *Lateriobtutus*

Pandanus biakensis, sp. nov.

Fig. 1, *a–g*, 2–5

Arbor 16 m. alta 25 cm. diametro (8 m. ex basi), corona ampla, trunco magno cortice spinosa, foliis 3.65 m. longis 15 cm. latis ligulatis planis in apice longe diminuentibus in 10 cm. ex apice 10 mm. latis, marginibus basalibus cum aculeis 2.5–3 mm. longis 4–9 mm. distantibus salientibus vel adscendentibus, marginibus medialibus cum aculeis 1.5–2 mm. longis 4–6 mm. distantibus adpressi-adscendentibus, marginibus apicalibus cum aculeis 0.5–1 mm. longis 1–3 mm. distantibus adpressi-adscendentibus, midnervio in pagine inferiori in basi inermi, in medio cum aculeis 0.5–1 mm. longis 8–19 mm. distantibus, proxime apice ad eas marginales simulantibus, syncarpiis 42–51 cm. longis 25–29 cm. diametro 14–24.36 kilo ponderatis terminalibus solitariis adscendentibus ovoideis, phalangibus 160–212 et 10.5–12.6 cm. longis 4–5.5 cm. latis 3.5–5.5 cm. crassis oblanceo-oblongis luteis lateribus cum angulis longitudi-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nalibus numerosis projectis et sulcis alternatis vadosis, superficie sublucida et in sicca brunnea, parte supera ⅓ libera, in sectio transverso quadrato vel pentagono, apice lata et vadositer concavo-truncata, carpelis 6–9 plerumque 7 apicibus truncatis vadositer concavisque eis centralibus tessellatis, sinibus centralibus subnullis, stigmatibus 1.5–2 mm. longis oblique ellipticibus et cum sinu basali centrali, carpela proxima breviore phalangis quisque focum est et stigmatibus alteris omnibus ad carpelam proximam singularem dirigitis, endocarpio paene submediali osseosi pallide brunneo marginibus 3–4 mm. latis, seminibus 14 mm. longis, 3 mm. diametro anguste ellipsoideis, mesocarpio apicali grandi ⅓ parte phalangis repletenti et indivisi multifibrosi et brunneo-medulloso membranoso, mesocarpio basali fibroso et carnoso.

Tree 16 m. tall, 25 cm. in diameter at the widest part (8 m. up the trunk), with ample crown; the bark slightly muriculate; prop roots 4–6 m. long, 10 cm. in diameter, spiny; leaves 3.65 m. long, 15 cm. wide, ligulate, plane, the apex slender and long tapering, at 10 cm. below the apex only 10 mm. wide; the margins near the base with salient or ascending stout prickles 2.5–3 mm. long, 4–9 mm. apart; near the middle the teeth 1.5–2 mm. long, 4–6 mm. apart, appressed ascending; near the apex the teeth 0.5–1 mm. long, 1–3 mm. apart, appressed ascending; the midrib below unarmed at base, at the middle with ascending prickles 0.5–1 mm. long, 8–19 mm. apart, but near the apex like those of the adjacent margins; fruiting heads terminal, single, ascending, ovoid, 42–51 cm. long, 25–29 cm. in diameter, weighing 14–24.36 kilos; phalanges 160–212 in number, 10.5–12.6 cm. long, 4–5.5 cm. wide, 3.5–5.5 cm. thick, oblance-oblong, yellow, the sides with numerous sharp, longitudinal ridges and alternating shallow furrows, the surface sublucid, when dried brown, upper ⅓ part free, in cross-section quadrate or pentagonal, the broad apex shallow concave-truncate; carpels 6–9, mostly 7, their apices truncate and shallowly concave, the central ones tessellate, their sinuses nearly lacking; stigmas 1.5–2 mm. long, oblique, elliptic, with a basal central cleft, the proximal carpel of each phalange the shorter and with the stigma facing distally, and all the other carpels oriented to and facing this focus carpel; endocarp slightly submedian, bony, pale brown, its margin 3–4 mm. thick; seeds 14 mm. long, 3 mm. in diameter, narrowly ellipsoid; apical mesocarp one large undivided area occupying ⅓ of the phalange, traversed by numerous fibers and with many membranous, brown cross-partitions, enclosed by a marginal prolongation of the endocarp; lower mesocarp fibrous and fleshy.

FIG. 2. *Pandanus biakensis*, holotype, in situ.

NOM. VERN.: "andim" (Biak); "diem" (Kurudu). Informant: Thimotaeus Samber of Biak.

HOLOTYPUS: Netherlands Nieuw Guinea, Biak I., 7 km. n. of Bosnek, in forest of bamboo, *Cyathea*, and *Ervatamia*, 60 m. alt., trees planted in forest edge, said to have been imported from Japen Is., 8 Dec. 1957, *H. St. John 26,142* (BISH).

FIG. 1. *Pandanus biakensis*, from the holotype. *a*, Leaf base underside, × 1; *b*, leaf base margin, × 4; *c*, leaf middle underside, × 1; *d*, leaf tip underside, × 1; *e*, phalange, lateral view, × 1; *f*, phalange, median longitudinal section, × 1; *g*, phalange apex, × 2.

DISCUSSION: The new section *Lateriobtutus* will receive several other species, but it is here based on a single species. It is distinctive in its shorter single or single line of proximal carpels which are the focus of the stigmas of all the other carpels of each large, oblong phalange. In the related section *Pandanus*, the stigmas are centripetal, focusing on the one or more central carpels, and the phalanges tend to be symmetrical.

SECTION *Australibrassia*

Pandanus conicus sp. nov.
Fig. 6

DIAGNOSIS HOLOTYPI: Arbor 10 m. alta laxe ramosa, trunco cum spinis adscendentibus armato, radicibus inclinatis aereis 40–50 cm. longis gracilibus multis, foliis 300–325 cm. longis in base 4.5 cm. latis ligulatis subcoriaceis ad basem inermibus supra glaucis in sectio transverso late M-formato sed 10 cm. ex base cum aculeis 1–2 mm. longis 5–10 mm. distantibus crassiter subulatis adscendentibus pallidis sed apicibus rubris midnervio inerme, in sectio mediale marginibus cum aculeis 0.6–1.5 mm. longis 3–10 mm. distantibus subulatis subadpressis pallidis cum apicibus rubris midnervio infra cum aculeis paucis minutis remotis, apice gracile et in sectio 10 cm. ex apice solum 1.2 mm. lato marginibus cum serris 0.5 mm. longis 2–3 mm. distantibus subulatis pallidis cum apicibus rubris midnervio cum dentibus simulantibus 0.5–0.7 mm. longis, syncarpiis solitariis pendentibus 24 cm. longis 16 cm. diametro elliptico-ovoideis, phalangiis ca. 44 et 6–6.2 cm. longis 4–4.4 cm. latis 3.4–3.8 cm. crassis pyriformibus compressis 4–6-angulatis lateribus laevibus curvatis sublucidis suturis lateralibus nullis parte dimidia supera libera apice 1–2.5 cm. lato truncato, carpellis 12–14, apicibus liberis 4–6 mm. longis anguste pyramidalibus acute angulosis eis centralibus erectis eis exterioribus cum capite erecto vel paene divergente vel inflexo, sinibus apicalis centralibus 4–6 mm. profundis, stigmatibus 1–2 mm. longis irregulariter ovalibus vel rhombicis obscure brunneis firmis lucidis apicalibus et plusminusve in lateribus ambis interioribus ex-

FIG. 3. *Pandanus biakensis*, holotype, spread of spiny prop roots at base. The tree was climbed on steps cut in a spiny prop root, seen to the right of center.

FIG. 4. *Pandanus biakensis*, holotype, syncarp, lateral and median views; also a view of the lower side and base of a leaf.

terioribusque prolapsis in latere proximo sulcatis supra sulcum proximum carpelli, endocarpio paene supramediale osseoso grande obscure mahogani-brunneo marginibus 3–5 mm. crassis, seminibus 10–12 mm. longis 3–4 mm. diametro ellipsoideis, mesocarpio apicale caverno unico fibroso meduloso formante, mesocarpio basale fibroso et carnoso.

DIAGNOSIS OF HOLOTYPE: Tree about 10 m. tall, "armed with stout, upturned prickles," crown open; prop roots 40–50 cm. long, slender; leaves 2.7–3.25 m. × 4.4 cm., "glaucous above at the base," ligulate but very gradually tapering to an elongate subulate tip which 10 cm. down from the tip is only 1 mm. wide; blade firm, subcoriaceous, the very base unarmed, not dilated, but near the base (beginning 10 cm. up) the margins with prickles 1.5–2 mm. long, 5–9 mm. apart, stout subulate, the tip pale, the base brownish, ascending at 45°, the nearby midrib smooth; at the middle the margins with teeth 0.7–1 mm. long, 2–7 mm. apart, ascending at 30°, stramineous or tipped with brown, the nearby midrib below with a few remote, very minute, appressed ascending spines; near the tip the margins and midrib below serrate with ascending spines 0.3 mm. long, 2–4 mm. apart; peduncle at least 14 cm. long, leafy bracted; fruiting syncarp about 24 cm. long, 16 cm. in diameter, elliptic-ovoid, pendent, bearing about 45 phalanges; phalanges 6–6.2 cm. long, 4–4.5 cm. wide, 2.8–3.5 cm. thick, slightly compressed, sharply 4–5-angled, each side between the angles a curving plane, somewhat shining, when dried brown, upper ½ part free, rounded, or just below the carpel apices slightly concave, the apex truncate (or very slightly convex); carpels 12–14 on lateral and principal phalanges, their carpel apices pyramidal, forming a flat top about 2.5 cm. wide; the outer ones strongly curving inflexed, the inner ones slender pyramidal, almost symmetrical, with numerous prominent angles; stigmas centripetal, running from the apex down the proximal side, those of marginal carpels 2 mm. long, narrowly elliptic, creased, those of central carpels 2–3 mm. long, narrowly elliptic to elliptic, dark, firm, creased

throughout; endocarp slightly above the middle, bony, massive, dark mahogany brown, the lateral margins 4–7 mm. thick; seeds 12–14 mm. long, 4–5 mm. in diameter, ellipsoid; apical mesocarp with one large cavern with pithy pale membranes and traversed by strong fibers; lower mesocarp fibrous and fleshy.

HOLOTYPUS: Australia, Queensland, Leo Creek, Upper Nesbit River, Cape York Peninsula, frequent and more or less gregarious, in rain forest, 420 m. alt., Aug. 16, 1948, *L. J. Brass 19,866* (Brisbane).

DISCUSSION: *P. conicus* is allocated to a new section. It is related to *P. cochleatus* St. John, here described. A statement of the contrasting differences is to be found in the treatment of that species.

The new specific epithet is from the Latin *conicus*, conical, in allusion to the shape of the projecting carpel tips. The sectional name is coined from Australia, plus Brass, the name of the collector, in tribute to the numerous and excellent collections of *Pandanus* and other genera that he has made.

In describing the lobed tips of phalanges composed of several partly united carpels, it is important to describe intelligibly the kind of lobing. Too many species have been described with phrases like, shallowly lobed, deeply lobed, with narrow sinuses, or with shallow sinuses, though all of these are almost meaningless. A complication is that often the sinuses gradually deepen as they approach the outer edges of the summit of the phalange. For use in this revision, the writer had adopted the method of measuring the depth of the apical central sinuses. The distance is measured from the bottom of the sinus up to a horizontal line even with the bottom of the stigma of the nearest carpel. A measurement could be taken to the top of the stigma, and this would also be usable. However, the stigmas are the softest part of a dried phalange, are exposed, and in a large per cent of the museum specimens are more or less eroded. Hence the measurement to the base is preferred. This measurement has been tested on scores of species and found to provide a character and one usually of diagnostic value.

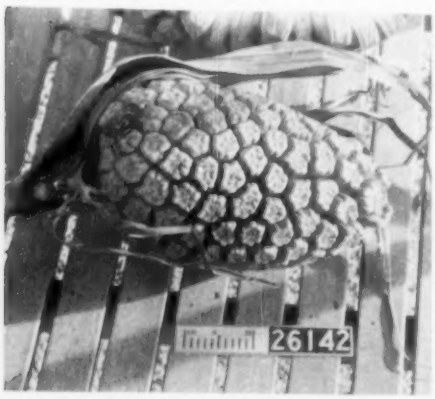


FIG. 5. *Pandanus biakensis*, holotype, lateral view of syncarp.

Pandanus cochleatus sp. nov.
Fig. 7

DIAGNOSIS HOLOTYPI: Arbor 4–5 m. alta laxe ramosa, radicibus aereis nullis, foliis 1–1.2 m. longis 3.2 cm. latis subcoriaceis ligulatis nervis secundariis fortibus nullis paene in apice subulato diminuentibus supra perglaucis infra ad basim perglaucis in base integris sed ad 10 cm. ex base dentibus 1.3–2 mm. longis 2–6 mm. distantibus subulatis stramineis sed in apice brunneis, midnervio inerme, in sectio mediali marginibus cum dentibus 0.5–1 mm. longis 1–2.5 mm. distantibus subulatis adscendenti-adpressis tum midnervio cum dentibus simulantibus 0.3–0.5 mm. longis 2.5–8 mm. distantibus, ad apicem marginibus cum serris 0.3–0.4 mm. longis 1–2 mm. distantibus adscendentibus sed in midnervio serris 2–8 mm. distantibus, syncarpiis ca. 13 × 11 cm. solitariis pendentibus ovoideo-globosis, phalangiis multis 4.3–4.5 cm. longis 3.3–4.2 cm. latis 2.4–3.3 cm. crassis (sed in phalangio duplicato 4.1 × 5.7 × 3.3 cm.) pyriformibus compressis apice truncato dimidio tam lato quam phalangio 4–6-angulosis suturis lateralibus nullis lateribus laevibus curvatis in sicco pallide brunneis sublucidis parte 3/5 supera libera, carpellis 12–16 (28 in duplicato) apicibus 4.5–7 mm. longis in summo phalangis truncato centrale aggregatis anguste compresso-pyramidalibus eis marginalis arcuatis incurvatis acute angulosis eis centralibus symmetricis et plerumque angustioribus, sinibus apicalis centralibus 4–6 mm. profundis, stigmatibus 1–1.5 mm. longis centri-

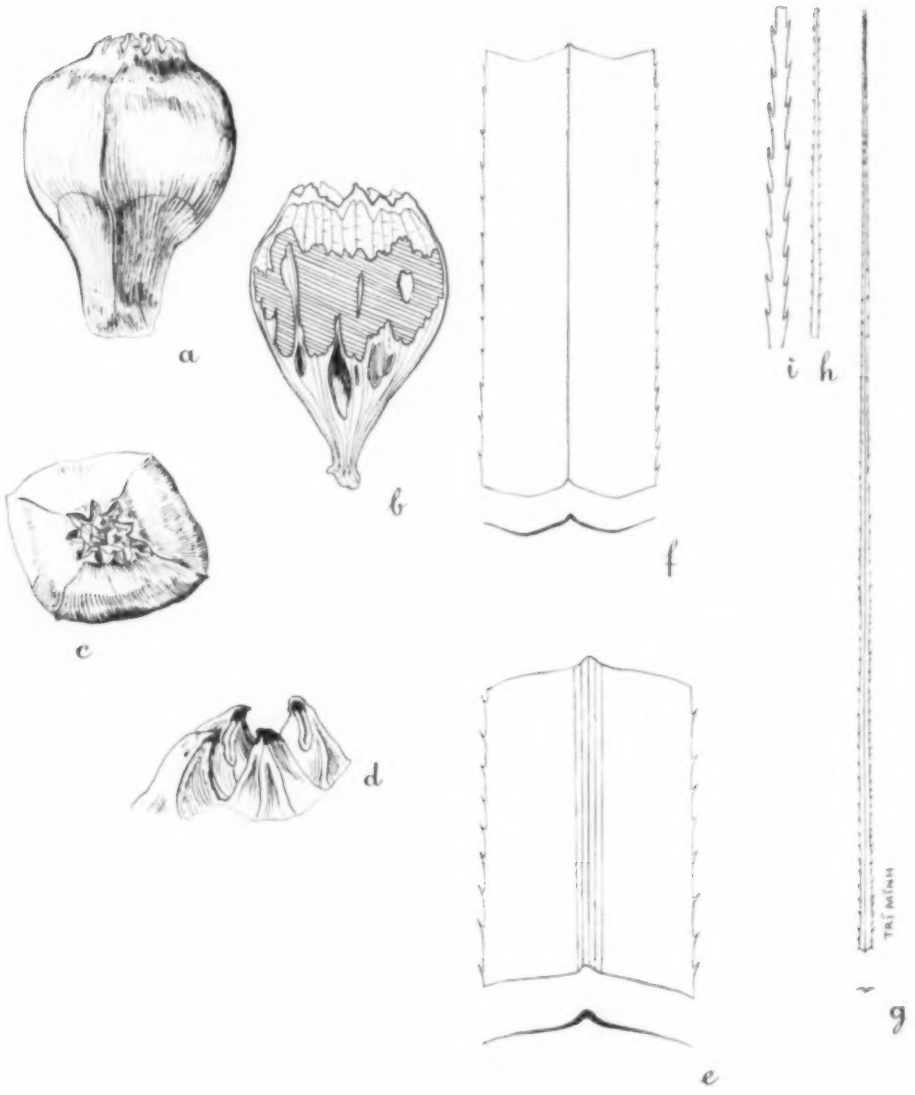


FIG. 6. *Pandanus conicus*. holotype. *a*. Phalange, lateral view, × 1; *b*. phalange, longitudinal section, × 1; *c*. phalange, apical view, × 1; *d*. carpel apices and stigmas, an inner one at lower right, and three outer ones, oblique view, × 4; *e*. leaf base, lower side, × 1; *f*. leaf middle, lower side, × 1; *g*. leaf tip, lower side, × 1; *h*. leaf tip, lateral view, × 1; *i*. leaf tip, lateral view, × 4.

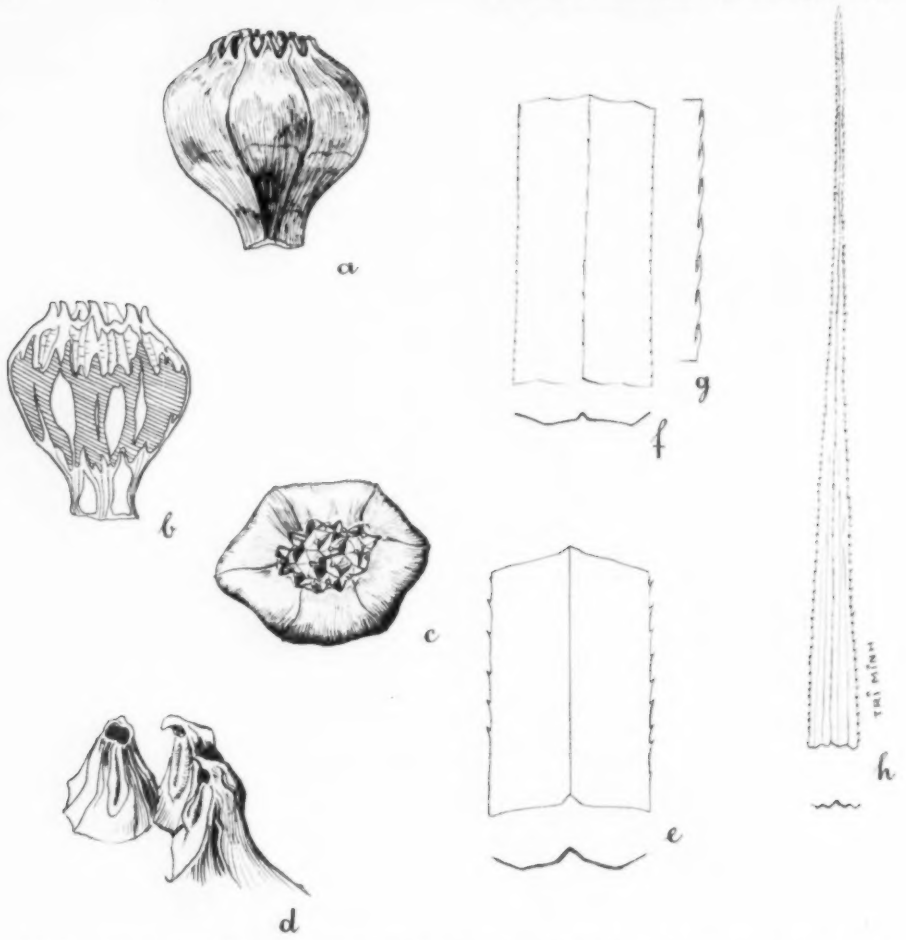


FIG. 7. *Pandanus cochleatus*, from holotype. *a*, Phalange, lateral view, × 1; *b*, phalange, longitudinal section, × 1; *c*, phalange, apical view, × 1; *d*, carpel apices and stigmas, an inner one at left, and two outer ones, oblique view, × 4; *e*, leaf base, lower side, × 1; *f*, leaf middle, lower side, × 1; *g*, leaf margin at middle, × 4; *h*, leaf apex, lower side, × 1.

petalibus ovalibus vel suborbicularibus sulcatis nigris apicalibus vel subapicalibus in latere proximo apicis affixis et infra apice pallido cartilagineo cochleato, apice proximo carpellis infra stigmate sulco pallido prominento ferrento, endocarpio mediale osseoso grande mahogani-brunneo lateribus 3–5 mm. crassis, seminibus 12–14 mm. longis 3–5 mm. diametro ellipsoideis, mesocarpio apicalis cum cavernis multis angustis medullosis et cum fibris validibus, mesocarpio basalis fibroso et carnoso.

DIAGNOSIS OF HOLOTYPE: "Tree, 4–5 m. tall; stem branched into a tiered, open crown; prop roots absent; leaves 1–1.2 m. long," 3.2 cm. wide, subcoriaceous, ligulate, with only one strong nerve, gradually long tapering to a subulate apex, this only 3 mm. wide at 10 cm. from the apex, "above very glaucous and below very glaucous at base," at base the margins entire for 6–10 cm., then with teeth 1.3–2 mm. long,

2–6 mm. apart, ascending at 45°, subulate, stramineous but brown-tipped, the basal midrib unarmed; the margins in the midsection with teeth 0.5–1 mm. long, 1–2.5 mm. apart, subulate, ascending, closely appressed, of the same color, the nearby midrib with similar teeth only 0.3–0.5 mm. long, 2.5–8 mm. apart; near the apex the margins with subulate-tipped serrations 0.3–0.4 mm. long, 1–2 mm. apart, ascending, of the same color, the adjacent midrib below with similar teeth 2–8 mm. apart; syncarps about 13 × 11 cm., solitary, pendent, ovoid-globose; phalanges numerous, 4.3–4.5 cm. long, 3.3–4.2 cm. wide, 2.4–3.3 cm. thick (but in a doubled one 4.1 × 5.7 × 3.3 cm.), pyriform, laterally compressed, the truncate apex about ½ as broad as the phalange, 4–6-angled, lateral sutures none, the sides smooth, curved surfaces, when dried light brown, somewhat shiny, upper 3/5 free; carpels 12–16 (28 in a double), crowded in a flat central apex, the tips 4.5–7 mm. long, narrowly compressed pyramidal, the marginal ones arcuate, incurving, sharply angled, the inner ones symmetric and mostly narrower, the central apical sinuses 4–6 mm. deep; stigmas 1–1.5 mm. long, centripetal, oval to suboricular, creased, black, apical or subapical, flush on the inner side of the conical apex below an overhanging, cartilaginous, pale, cochleate tip; below the stigma the proximal crease on the carpel is prominent and with pale liplike edges; endocarp median, bony, extensive, mahogany brown, the lateral margins 3–5 mm. thick; seeds 12–14 mm. long, 3–5 mm. in diameter, ellipsoid; apical mesocarp with numerous narrow caverns traversed by strong fibers and pale medullary partitions; basal mesocarp fibrous and fleshy.

HOLOTYPUS: Australia, Queensland, Cape York Peninsula, Brown's Creek, Pascoe River, frequent in brushy forest on islands in flood bed of creek, 60 m. alt., July 13, 1948, *L. J. Brass 19,540* (BRISBANE).

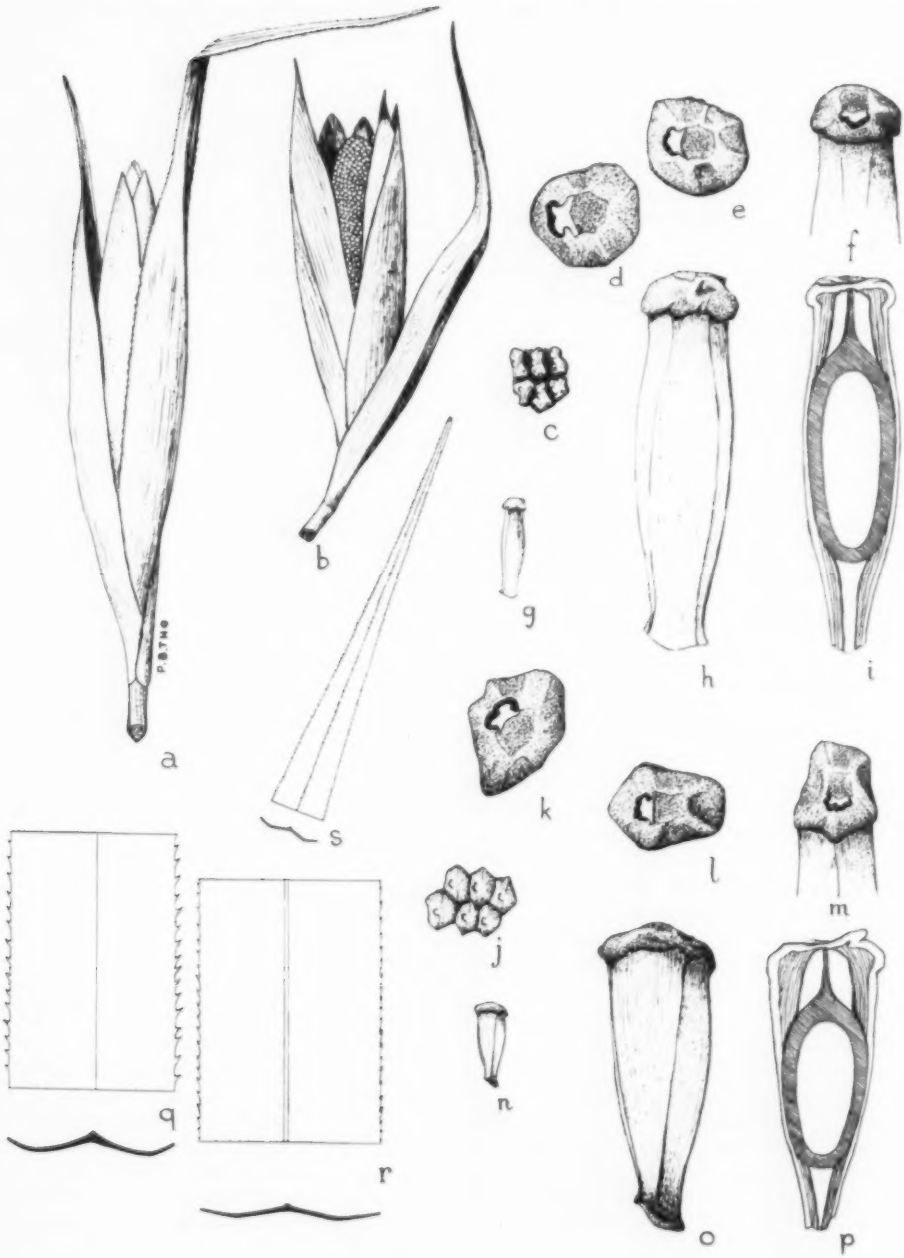
DISCUSSION: *P. cochleatus* is a member of the section *Australibrassia* which is a segregate from the section *Vinsonia*. Its closest relative is the Australian *P. conicus* St. John, from which it differs by having the prop roots absent; leaves 1–1.2 m. long, 3.2 cm. wide, at midsection the marginal teeth 1–2.5 mm. apart; syncarp 13 × 11 cm., ovoid-globose; phalanges 4.3–4.5 cm. long, the upper 3/5 free; stigmas apical or subapical, flush on proximal side of carpel apex, under an overhanging cartilaginous cochleate tip; and the endocarp median. On the other hand, *P. conicus* has prop roots 40–50 cm. long, slender, numerous; leaves 3–3.2 m. long, 4.5 cm. wide, at midsection the marginal teeth 3–10 mm. apart; syncarp 24 × 16 cm., elliptic-ovoid; phalanges 6–6.2 cm. long, the upper ½ free; stigmas apical and overlapping on both proximal and distal sides of carpel apex; and the endocarp supramedian.

The new epithet is from the Latin *cochlea*, sea shell or snail shell, an allusion to the shell-like carpel apex that overhangs the stigma.

SECTION *Maysops*

Pandanus Zea sp. nov.
Fig. 8

DIAGNOSIS HOLOTYPI: Arbor 10–12 m. alta ramosa cum radicibus fulturosis longis trunco radicibusque cum aculeis parvis adscendentibus armatis, foliis 1.5 m. longis 4.2 cm. latis coriaceis ligulatis in sectio M-formatis in apice subacuto longiter diminuentibus et in puncto 10 cm. ex apice 14 mm. latis infra pauce glaucis ad basim marginibus cum subulato-serris 1.5–2 mm. longis 2–4 mm. distantibus in 45° adscendentibus in apicibus brunneis midnervio exarmato, in regio mediale marginibus cum subulato-serris 0.8–1 mm. longis 2–5 mm. distantibus in 25° adscendentibus in apicibus brunneis midnervio exarmato, ad apicem marginibus cum subulato-serris 0.3–1 mm. longis 0.5–2 mm. distantibus, midnervio cum serris simulantibus sed distantioribus, pedunculis foliosis, syncarpiis solitariis subpendentibus cum bracteis numerosis aurantiaco-luteis amplectentibus et fructu *Zea Mays* simulantibus, corpore ca. 33 × 5.5 cm. apice acuminato viride 20 cm. longo in sectio mediale cum dentibus aciculatis salientibus 1–1.5 mm. longis, bracteis interioribus coloratis navicularibus ellipticis 35 cm. longis 9.5 cm. latis in tertia infera cum dentibus aciculatis salientibus 1–2 mm. longis 1–2 mm. distantibus, in sectio mediale exarmatis, in tertia supera marginibus et nervo mediale cum dentis subulatis 0.6–0.9 mm. longis 0.5–1 mm. distantibus adpresse adscendentibus, syncarpiis 20–22 cm. longis 7–7.5 cm. diametro cylindricis obtusis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luteis, drupis biformatis eis terminalibus 14–17 mm. longis 5.5–9 mm. latis 5–8 mm. crassis oblanceoloideis pileo 1–2 mm. alto, stigmate 1–1.5 mm. latis exterminalibus lunatis brunneis in apice syncarpi dirigito horizontale infra sed exserto ex projectione cartilagineo luteo flabellato sed plerumque 1- 2-lobato, endocarpio centrale 9 mm. longo lateribus 1 mm. latis pallidis duris cartilagineis sed faciliter in fibris transversis fractis, drupis lateralibus 20–21 mm. longis 4–5 mm. latis 3.5–4.5 mm. crassis corpore oblongo-fusiforme, pileo 2–3 mm. alto depresso convexo marginibus sinuatis, mesocarpio apicale caverno unico formato, mesocarpio basale in centro cavernoso in lateribus fibrosis.

DESCRIPTION OF ALL SPECIMENS EXAMINED: Tree 7–12 m. tall, branched into an open crown, supported on prop roots about 1 m. long, the stem and roots "armed with small, sharp, upturned prickles"; leaves 1.5–1.72 m. long, 4.1–4.2 cm. wide, coriaceous, M-shaped in cross-section, ligulate, long tapering to subacute tip, and 10 cm. back from tip only 14 mm. wide, the lower side somewhat glaucous, almost to the base the margins with subulate-tipped serrations 1.5–2 mm. long, 2–4 mm. apart, ascending at 45°, tipped with brownish, the midrib unarmed, at the middle the margins subulate-serrate, the teeth 0.8–1 mm. long, 2–5 mm. apart, ascending at 25°, brownish tipped, the midrib unarmed, near the tip the margins subulate-serrate, the teeth 0.3–1 mm. long, 0.5–2 mm. apart, the midrib below with similar but more remote teeth; peduncles leafy bracted; syncarps solitary, subpendent, surrounded and completely enwrapped by numerous orange-yellow bracts, and strongly resembling an ear of corn in its husk, the two outer bracts with the body about 33 × 5.5 cm., then prolonged into an acuminate, green tip about 20 cm. long which resembles the leaves, at midsection the salient, acicular teeth 1–1.5 mm. long; inner colored bracts boat-shaped, elliptic, 35 cm. long, 9.5 cm. wide, margins of the lower third with acicular, salient teeth 1–2 mm. long, 1–2 mm. apart, the middle unarmed, the upper third with the margins and midrib with teeth 0.6–0.9 mm. long, 0.5–1 mm. apart, subulate, appressed ascending; syncarps 20–22 cm. long, 7–7.5 cm. in diameter, cylindric, obtuse, yellow; drupes of two shapes, the terminal ones 14–17 mm. long, 5.5–9 mm. wide, 5–8 mm. thick, oblanceoloid, ending in the low convex pileus 1–3 mm. high; stigma 1–2 mm. wide, on pileus but off center, lunate, brown, facing apex of syncarp and at right angles to drupe, projecting from under a cartilaginous, yellowish visor, fan-shaped but usually with 1–3 rounded lobes; endocarp central, 9–10 mm. long, the sides 1–1.5 mm. thick, pale, hard, cartilaginous but easily broken into transverse fibers; lateral drupes 20–21 mm. long, 4–5 mm. wide, 3.5–4.5 mm. thick, the body oblong fusiform, the pileus 2–3 mm. high, low convex, its lower margin scalloped; apical mesocarp a single cavern; basal mesocarp cavernous in the center, fibrous on the sides.

HOLOTYPUS: Australia, Queensland, Cape York Peninsula, Iron Range, common in hollows and gullies in rain forest, 20 m. alt., June 22, 1948, *L. J. Brass 19,293* (BRI).

SPECIMENS EXAMINED: Australia, Queensland, Cape York Peninsula, Leo Creek, Upper Nesbit River, frequent in a ravine in rain forest, 420 m. alt., Aug. 16, 1948, *L. J. Brass 19,869* (BRI).

DISCUSSION: The closest relative is *P. amboinensis* Warb. of the East Indies which has the leaf margin near the base with divergent spines, the midrib spiny near the base and at the middle; pileus apex truncate; stigma under a projecting entire tooth; and the endocarp supramedian. On the contrary, *P. Zea* has the leaf margin near the base with ascending spines, the midrib unarmed near base and middle; syncarp concealed; pileus apex convex; stigma under a projecting 2- 3-lobed tooth; and the endocarp inframedian.

The specific epithet is the generic name *Zea* of the cultivated corn or maize, chosen because of the similarity of the fruits.

FIG. 8. *Pandanus Zea*, holotype. *a*, Younger syncarp, × 2/7; *b*, mature syncarp, × 2/7; *c*, lateral drupes from above, × 1; *d,e*, lateral drupe from above, × 4; *f*, lateral drupe from side, × 4; *g*, lateral drupe, side view, × 1; *h*, lateral drupe, side view, × 4; *i*, lateral drupe, longitudinal section, × 4; *j*, apical drupes, from above, × 1; *k,l*, apical drupe from above, × 4; *m*, apical drupe, oblique lateral view, × 4; *n*, apical drupe, lateral view, × 1; *o*, apical drupe, lateral view, × 4; *p*, apical drupe, longitudinal section, × 4; *q*, leaf base, lower side, × 1; *r*, leaf middle, lower side, × 1; *s*, leaf apex, lower side, × 1.

Studies on Pacific Ferns
Part I. Nomenclature Changes and Distributions of Some Species of *Hymenophyllum, Arthropteris, Microlepia, Oleandra,* and *Adiantum*

G. BROWNLIE[1]

DURING A PERIOD OF STUDY at the Herbarium of the Royal Botanic Gardens at Kew the author spent some time examining collections of ferns from the South Pacific area. It was quickly apparent that in most groups there is some confusion in interpretation of the various species, and the following paper is an attempt to clear up some of these points.

GENUS *Hymenophyllum*

Differences between the specimens examined and the descriptions appearing in Copeland's revision of the genus were noted in some small species of *Hymenophyllum* (sens. lat.). Consequently a detailed examination of this group was undertaken, with particular reference to those species possessing fronds with serrated margins which Copeland distinguished as *Meringium* and *Hymenophyllum*. The following observations, which are the result of these investigations, amount to a further revision of this group for the South Pacific region, excluding Australia and New Zealand. The present author prefers to retain, in the meantime, the generic name *Hymenophyllum* for all the species concerned, as he is not convinced of the validity of Copeland's distinguishing characters.

FIJI

Hymenophyllum affine Brack.

Hymenophyllum affine Brack. Expl. Exped. 16, 265, 1854.
Trichomanes macgillivrayi Bak. Ann. Bot. 5, 195, 1891.

The original description of this Fijian species by Brackenridge states "sori few on upper half of the fronds—two-valved for ⅔ of its length, obovate, lips entire,—receptacle short, included," while Baker describes his species as "sori one to a pinna near the base on the upper side—indusilum with a campanulate tube and suborbicular entire lips." These two descriptions are not dissimilar, and a comparison of Baker's type material with the illustrations of Brackenridge's specimen tends to support the idea that these two are in fact the same species. Baker's statement that his material was glabrous is not supported by an examination of the type, which has hairs on the stipe, lower rachis, and rhizome similar to those illustrated by Brackenridge. The difference in size between the two forms described is bridged by later collections from Fiji, and Baker's specimen seems to be a large example only.

Specimens examined (all from Fiji): McGillivray unnumbered (Kew, Baker's type); Parks 20040 (Kew, B.M.[2]); A. C. Smith 1368 (Kew); H.M.S. Herald Bot. No. 138 (Kew); H.M.S. Herald Bot. No. 286 (Kew).

Hymenophyllum pseudotunbridgense Watts.

Hymenophyllum pseudotunbridgense Watts. Proc. Linn. Soc. N.S.W. 39, 766, 1915.
Hymenophyllum macgillivrayi (Bak.) Copel. Philipp. J. Sci. 64, 60, 1937.

In his section on *H. macgillivrayi* Copeland quotes Baker's description of *Trichomanes macgillivrayi*, and supplements this with a further description based on a collection by J. Horne 1877–78, illustrating this on plate 38. This illustration perfectly matches further Horne material at Kew which is distinct from Baker's *T. macgillivrayi*. The involucre is longer and

[1] Botany Department, University of Canterbury, Christchurch, New Zealand. Manuscript received April 20, 1959.

[2] British Museum (Natural History).

narrower in the Horne material and the receptacle is markedly extruded. Copeland has thus confused two quite distinct Fijian species under the name *Hymenophyllum macgillivrayi*. A comparison of the Horne material with species from surrounding areas shows that it is almost identical with *H. pseudotunbridgense* from Queensland, and consequently this name should be given to the form illustrated by Copeland as *H. macgillivrayi*.

Specimens examined (all at Kew): Queensland, Bailey unnumbered; Fiji, Horne 983 in part, 1076, and unnumbered; A. C. Smith 5713.

Hymenophyllum denticulatum Sw.

Hymenophyllum denticulatum Sw. Schrad. Journ. 1800/2, 10, 1801.

This species is quite distinct from all other small Fijian members of the genus in the possession of a conspicuous wing along the whole rachis.

NEW CALEDONIA

Hymenophyllum subdimidiatum Ros.

Hymenophyllum subdimidiatum Ros. Meded. Rijks-Herb. Leiden no. 11, 1, 1912.
Hymenophyllum viride Ros. Copel. Philipp. J. Sci. 64, 59, 1937.

In his treatment of this species Copeland quotes Rosenstock's description and mentions the type material as Schlechter 14799, which he states he has not seen, but in the same paper he publishes the new species *H. viride* from material with the same collection number. The plate illustrating this species shows it to be the same as Rosenstock's original description and the same as a cotype (Schlechter 14799) at Kew.

It is doubtful whether or not this species is distinct from *H. pseudotunbridgense*, for, although no markedly extruded receptacles were noted, the involucre shape is the same and the general appearance of the plant is very similar. However, until a greater amout of comparative material is available it is perhaps better to retain the species.

Material examined: Schlechter 14799 (Kew); Balansa 2701 (Kew, B.M.).

Hymenophyllum dimidiatum Mett.

Hymenophyllum dimidiatum Mett. Kuhn. Linn. 35, 393, 1868.

This species is somewhat larger than the preceding one and is distinct in the possession of a serrated involucre. An examination of the type material shows this fern is not glabrous, as appeared in the original description, but has hairs on the stipe and rachis. In fact, no glabrous species was noted among the groups discussed in this paper.

Specimens examined: Deplanche in Herb. Lenormand (Caen); Vieillard 2258 (Kew, B.M.).

Hymenophyllum piliferum C. Chr.

Hymenophyllum piliferum C. Chr. Vjschr. Naturf. Ges. Zürich 70, 221, 1925.

Christensen separated this from *H. dimidiatum* on the basis of the hairs on stipe and rachis but, as noted above, the type material of that species is not glabrous. However, it is felt that it should be retained as a valid species on the grounds of its more open growth form and much smaller size. It is similar to *H. subdimidiatum* in form and size but has the serrated involucre of *H. dimidiatum*. Copeland included specimens assigned to this by Christensen in his examples of *H. dimidiatum* and ignored Christensen's species completely.

Specimens examined: Franc 1450 in Herb. C. Christensen (B.M.); Rosenstock 133 (B.M.).

Hymenophyllum pumilio Ros.

Hymenophyllum pumilio Ros. Fedde Repert 9, 72, 1910.

This is a very reduced species somewhat similar to *H. minimum* of New Zealand, but lacking the spines found on the sides of the sorus in that species. It cannot be confused with any other New Caledonian fern.

SAMOA

Hymenophyllum praetervisum Christ.

Hymenophyllum praetervisum Christ. Engl. Jahrb. 23, 338, 1896.

This is the only small species in this section

in Samoa and is quite distinct from the Fijian and New Caledonian forms in having the sori free from the pinnae and not in any way immersed.

LORD HOWE ISLAND

Hymenophyllum moorei Bak.

Hymenophyllum moorei Bak. Syn. Fil. 464, 1874.
Hymenophyllum pumilum C. Moore, Copel. Philipp. J. Sci. 64, 91, 1937 (in part).

Copeland united the Australian *H. pumilum* and the Lord Howe Island *H. moorei*, disregarding the distinctions noted by Baker in the original descriptions. A comparison of both types at Kew shows that the sori in the Australian material are terminal, not immersed at the base, and have valves slightly serrated at the apex, while the Lord Howe Island specimen has lateral sori, immersed at the base, and with conspicuously toothed valves. The distinction in position of the sori is alone sufficient to retain the two as separate species. Copeland's illustration (pl. 45) figures *H. moorei*, not *H. pumilum*.

Specimens examined: C. Moore unnumbered (Kew), Baker's type.

Hymenophyllum howense Brownlie n. sp.

Rhizoma longe repens, sparsis et rufis pilis ornatum; stipes filiformis, 2 ad 4 cm. longus, ad basem pilosus; frondes usque ad 5 cm. altae, 2 cm. latae, lineares ovatae, tri-quadri-pinnatifidae; segmentis usque ad 2 cm. longis, angustis linearibus, inconspicue serrulatis; sori in apicibus segmentorum breviorum, non immersi, indusio suborbiculari, labiis integris, receptaculo exserto.

Rhizome creeping, with scattered multicellular rugose hairs which sometimes occur in clusters at the base of the stipes and at branch junctions. Stipe filiform, 2–4 cm. long, with scattered hairs similar to those on the rhizome. Fronds up to 5 cm. long and 2 cm. wide at the widest point, linear-ovate in outline, flabellately 3 or 4 pinnatifid. Divisions narrow, linear, up to 2 cm. long, obscurely serrate. Sori mostly on upper half of frond, terminal on short segments, not immersed. Involucre suborbicular, cleft more than half way to the base. Lips entire, receptacle extruded.

Lord Howe Island, Mt. Gower, at a high altitude. C. Moore No. 4 (Kew).

This species is related to *H. pseudotunbridgense* Watts, but is distinguished by the relatively wide frond and very long, narrow segments. The segments are narrower and longer than those of *H. subdimidiatum* Ros., to which it also appears to be related.

The remainder of this paper consists of a varied assortment of ferns in which confusion exists either as to specific distinctiveness or as to geographical range.

Arthropteris neocaledonica Copel.

Arthropteris neocaledonica Copel. Sargentia 1, 4, 1942.

This has been distinguished from *A. tenella* (Forst. f.) J. Sm. by the possession of black instead of brown scales, and in having the position of the sorus well marked on the upper surface. An examination of collections at Kew shows the last character to be of doubtful value, but the distinctive colour of the scales is in fact consistent for all New Caledonian material. This contrasts very clearly with the light chestnut-brown scales of New Zealand and Norfolk Island specimens. Many of the collections from New Caledonia had previously been identified as *A. tenella*, and the geographical range of that species given in Christensen's "Index Filicum" includes that island, but the characteristic scale colouring was observed on all specimens from there. It seems best then to distinguish two species, geographically separated, *Arthropteris tenella* in New Zealand and Norfolk Island, and *A. neocaledonica* confined to New Caledonia.

Microlepia speluncae (L.) Moore var. *exserta* Mett.

Davallia speluncae var. *exserta* Hk. and Bak. Syn. Fil. 470, 1864.
Microlepia exserta Mett. Kuhn Linn. 36, 148, 1869; C. Chr. Ind. Fil. 426, 1906.

An examination of material of *M. speluncae* from the Pacific islands shows the distinguish-

ing character of this variety, the extruded receptacle, to be present only in some material from Fiji, and in that area the degree of extrusion varies considerably. Other Fijian specimens do not have the receptacle extruded at all. In view of the range noted in this character, and the fact that it is not consistent, it is better to regard this as no more than a variety restricted to Fiji.

Oleandra neriiformis Cav.

Oleandra ciliata Kl. Kuhn Linn. 36, 126, 1869; C. Chr. Ind. Fil. 466, 1906.

Christensen has already reduced many of the Pacific forms of *Oleandra* to synonyms of the widespread *O. neriiformis*, and an examination of a cotype of this species at the British Museum of Natural History shows that it does not go outside the range of characters now accepted for that species.

Adiantum novae-caledoniae Keys.

Specimens of *Adiantum* from New Caledonia seem to have been variously identified as *A. novae-caledoniae* Keys., *A. aneitense* Carr., and *A. fulvum* Raoul, without any clear idea as to the distinguishing characters, if any, of these three species. A detailed examination of material from Aneitum, New Caledonia, Norfolk Island, and New Zealand shows that they are not only easily distinguished morphologically, but are geographically isolated. All material from New Caledonia lacks rugose hairs on the upper surface of the pinnae, and the pinnules are usually markedly attenuated. These represent *A. novae-caledoniae*. Specimens from Aneitum also are glabrous on the upper surface and are subglaucous beneath, a character which is still very apparent in dried examples and which is not found in material from other areas. They also lack the definite lobing on the lower edge of the pinnules which is found in New Caledonian specimens. These form *A. aneitense*. *A. fulvum* as represented by material from New Zealand and Norfolk Island has rugose hairs on the upper surface of the pinnae, a character not noted in any material from New Caledonia ascribed to this species. A summary of this discussion is given here.

Rugose hairs on upper surface of pinnae.....*A. fulvum* (New Zealand and Norfolk Island).

Rugose hairs absent on upper surface:

Pinnae subglaucous beneath.....*A. aneitense* (Aneitum).

Pinnae not subglaucous beneath.....*A. novae-caledoniae* (New Caledonia).

SUMMARY

The small serrated-frond species of the genus *Hymenophyllum* are revised for the South Pacific islands region, and the morphological characters and distributions are clarified for one species of *Arthropteris* and three of *Adiantum*, while one species of *Oleandra* is reduced to synonymity, and a species of *Microlepia* is reduced to varietal rank.

ACKNOWLEDGMENTS

I wish to thank Mr. F. Ballard of the Herbarium, Royal Botanic Gardens, Kew, for his assistance with this work, and I acknowledge my indebtedness to the Council of the University of Canterbury for provision of the refresher leave during which it was undertaken.

Remarks on the Succession of Bryophytes on Hawaiian Lava Flows

HARVEY ALFRED MILLER[1]

THE HAWAIIAN ISLANDS are well known for their volcanic origin and for continuing volcanic activity on the largest island, Hawaii. On May 13, 1955, Hawaii experienced a volcanic eruption and lava flow of considerable magnitude. Professor Maxwell Doty undertook a series of surveys to outline the plant succession on this new flow.[2]

The first bryophyte was observed and collected at about a 950-ft. elevation on December 20, 1955, when a tiny juvenile colony of *Campylopus introflexus* (perhaps *C. boswelli*, though this species was not collected later) was discovered in the folds of lava blisters. A substantial portion of the collection was sent to me in half of a foil chewing-gum wrapper—which indicates the extreme youth of the colony. The individual plants were 3–5 mm. high, or about the length of 1½ leaves. On February 22, 1956, *Campylopus densifolius*, in about the same stage of development as the first moss collected, was taken at about 900 ft., in the Kamaili Homesteads at Puna. In late March more colonies of *C. densifolius* were discovered on the Iilewa flow, and *C. exasperatus* was discovered growing on old lava adjacent to the new flow. Specimens of apparently living *Macromitrium owahiense* were collected from the bark of a *Metrosideros* (*Ohia lehua*) tree which had been killed by the encroachment of hot lava. In August, *Campylopus introflexus* was found on the flow about ½ mi. east of McKenzie Park. In subsequent collections this species seemed to be established in several places on the new flow. Two species previously unrecorded for the Iilewa flow were discovered at about 950 ft. in April, 1957, and *Rhacopilum cuspidigerum* and *Rhacomitrium lanuginosum* var. *pruinosum* were added to the growing list of pioneer bryophytes. The December, 1958, collections contained *Campylopus exasperatus* and *Funaria hygrometrica*, along with species previously found on the flows.

In general, exposed lava flows support few species of bryophytes and these are restricted to protected crevices or small shaded niches. The several species of *Campylopus* establish themselves rather readily in lava under climatic conditions of the type favorable for the growth of *Metrosideros*. It is of interest that *Campylopus fumarioli* becomes established in the steam fissures at Kilauea. In Hawaii, species of *Campylopus* appear to play a significant pioneer role in rock succession and are often found on rocks devoid of other plants. *Rhacopilum cuspidigerum* is the most ubiquitous moss in Hawaii and with its obviously great range of tolerance would be expected to be a pioneer species on new lava as well as on older rocks. It produces an abundance of spores throughout the year, which is another factor favoring rather rapid establishment in unoccupied habitats in frost-free regions.

Rhacomitrium lanuginosum var. *pruinosum* has a much greater altitudinal range than *Rhacopilum* and is found in more exposed situations. The upper half of each leaf is hyaline and the striking silver-grey tufts of *Rhacomitrium* can be easily seen and recognized. Above 8,000 ft. on the barren lava flows of Mauna Loa this species of *Rhacomitrium* and *Grimmia trichophylla* are the only plants to be found. I have collected both of these mosses on the unexposed sides of lava clinkers at 11,000 ft. The *Rhacomitrium* has been collected at the summit of Mauna Loa by several people. In spite of its great tolerance of seemingly arid conditions, *Rhacomitrium* plays an important role in bog formation in the Alakai Swamp on Kauai. It is suggested that the acid nature of the bog may represent a physiologically, though not physically, arid habitat with the cloud moisture

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[2] This study was aided by NSF Grant G1922.

characteristic of mountain tops. Comparative physiological studies of several populations would be most interesting in this regard.

The species of *Campylopus, Rhacopilum, Rhacomitrium,* and *Grimmia* previously mentioned are true pioneers which establish themselves on bare lava rock. However, other mosses appear on relatively new lava flows in pockets where dust collects to form a minute patch of soil. The plants which colonize this type of microhabitat are mosses of world-wide distribution which might aptly be called "weeds." *Funaria hygrometrica* is the only such species found in Doty's collections, although *Bryum argenteum* and *Ceratodon purpureus* have been found on essentially barren lava flows in similar circumstances.

The classical concept of lichen–moss–herb–shrub–tree succession does not apply in Hawaii on new lava flows. Mosses are true rock pioneers and lichens are rather limited in their establishment. In general, a few species of bryophytes become established in suitable microhabitats and never form an extremely conspicuous part of the vegetation. In fact, it would seem to one who has observed Hawaiian lava flows that plants are established wherever and whenever suitable habitats exist for the disseminules which reach these habitats. Thus, no exact plant succession of one plant replacing another can be established. With the establishment of vascular plants, new microhabitats become available and such moss species as *Macromitrium brevisetum, M. emersulum, Fissidens* spp., *Bryum* spp., *Pohlia* spp., *Ectropothecium sandwichense,* and *Vesicularia graminicolor* become established on rock in mesophytic regions. Often the leafy liverwort *Brachiolejeunea sandvicensis* becomes established at the same time as the mosses listed above. Another liverwort, *Riccia rechingeri,* was recently discovered in soil pockets in the Kau desert and may be discovered in similar habitats on newer flows. As soil is necessary for the growth of this plant, it probably should not be considered a true pioneer species.

Mycorrhizal Infection of Germinating Seedlings of *Nothofagus solandri* var. *cliffortioides* (Hook f.) Poole

B. C. Arnold[1]

In the course of studying the anatomy of roots of the evergreen tree, *Nothofagus solandri* var. *cliffortioides*, regular observations were made on the natural germination of seedlings in a small tract of forest in the vicinity of the University of Canterbury Mountain Biological Station at Cass. The area concerned is about 2 acres in extent, at an altitude of 2,000 ft. above sea level, isolated in a gully from the main forest areas of *N. solandri* var. *cliffortioides* which dominate the wetter mountainous region a few miles to the west. Rainfall over a 12-month period was 47.9 in. The soil is a mixture of clay and greywacke covered by humus and moss. Growth of the seedlings was inspected at fortnightly intervals over a period of 18 months.

The mycorrhizas of *N. solandri* var. *cliffortioides* are similar in a general way to those of *Fagus sylvatica* (Harley, 1937: 421–423) but are somewhat smaller, and do not give rise to the "intense racemose" type (Harley, 1937: 421–423).

Four months after germination had commenced, a drought of more than 2 weeks was encountered, during which newly formed mycorrhizas shrivelled, many seedlings wilted, and a large proportion died. It was not apparent whether this circumstance had any radical influence on the degree or course of subsequent mycorrhizal infection.

Microscopic examination was made of intact root and mycorrhiza surfaces as well as of serial transections and longisections, in an attempt to follow the pattern of mycorrhizal infection of the seedlings. The present investigation was incidental to anatomical studies of mycorrhizas to be reported elsewhere.

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Germination and Infection

At the time of the emergence of the radicle, in spring, the blackened seed coat was generally enmeshed in mycelial threads of several different types. The testa was intact except at the point of emergence of the radicle, but in a state of superficial decay. In serial microtome sections of the seed, no sign of fungal infection of the expanding embryo was to be seen.

As the radicle grew ahead through moss or leaf mould, hyphae of different colour and form traced rather sparsely over the smooth surface of the root, which maintained a fairly constant diameter of about 0.75 mm. With the appearance of the piliferous layer, however, a more copious growth of fungi took possession of the radicle and became inextricably entangled in the elongating root hairs.

Clamp connections were evident in several of the different types of fungi. Among these was a species constantly present and notable for its long, solitary hyphae, even septation, distinct clamps, and thick golden-brown walls. This fungus appears to have no role in the formation of *N. solandri* var. *cliffortioides* mycorrhizas, although it may be a regular occupant of the rhizosphere of the tree.

Regions of the radicle lacking root hairs were less densely overgrown with fungi than was the piliferous zone.

After 3 or 4 weeks growth of the seedlings (by which time the cotyledons were well expanded), broad sheets of coherent hyphae, in roughly parallel strands, were found connecting the seedling roots with mycorrhizas of nearby trees, from which they had apparently emanated. Most of the fungal wefts joining old mycorrhizas and the root surface of seedlings were white or colourless. In the course of growth, the radicles came also in contact with violet, yellow,

and brown hyphae which nevertheless did not appear to lead to infection or any definite pattern of association.

Radicles in many cases achieved a length of 40 mm. without the appearance of branch roots. Up to this stage, no penetration of roots by hyphae was found though aggregates of mycelium formed in some cases a superficial collar-like layer anterior to the root-hair zone.

Invasion of the radicle had not so far begun.

After 6 or 7 weeks, usually at a time when leaves were expanding above the cotyledons, branch roots became obvious to the naked eye. A considerable proportion grew ahead free of infection, but others were attacked at the tips, as they emerged at the surface, by hyphae massed in a layer along the radicle. Microscopically the laterals so-enveloped by hyphae bore all the characteristics of mycorrhizas. As subsequent laterals reached the root exterior, some were transformed into mycorrhizas and others grew ahead, unimpeded, as nonmycorrhizal roots.

In microtome sections of the radicle, no indication was found of intracellular penetration between mature epidermal cells. In emerging branch roots, intracellular penetration between epidermal cells was found only following radial elongation of the cells of the epidermis. This modification of the epidermal cells appears to be a necessary preliminary condition for penetration by the mycorrhizal fungus. The prior aggregation of mycelium around the root-growing point to form a sheath appears to so alter the development of the epidermis as to enable later penetration.

From the earliest stages of mycorrhiza formation there was a tendency for the root apical meristem of thicker mycorrhizas to burst through the fungal mantle and to continue growth free of infection. Such recovery was not abundant at first but after 3 months became frequent.

By mid-summer, mycorrhizas were present on most seedlings, though most radicles and a proportion of branch roots remained uninfected.

MYCORRHIZAS OF TRANSPLANTED SEEDLINGS

Transplanted mycorrhizal seedlings which were grown out-of-doors in pots in a friable mixture of oak-leaf mould, sand, fine gravel, and loam, continued to form mycorrhizas of a large "simple" type (Harley, 1937: 421–423) over a period of 3 years.

With kitchen garden loams, results were variable. In heavier loams, large uninfected roots predominated. Mycorrhizas were abundant in lighter loams.

In pits of pure river sand, about 2 ft. deep and 3 ft. wide, set in sandy soil, numerous fine and often distorted roots were formed, but mycorrhizas were rare.

When mycorrhizal seedlings were transplanted to pots containing vermiculite watered with a nutrient solution, no mycorrhizas were found after 6 months. The solution used was a basal medium devised by Melin and Nilsson (1950: 89) for mycorrhizal pine seedlings, with glucose and thiamine omitted.

DISCUSSION

It appears that the mycorrhizal association in *N. solandri* var. *cliffortioides* reaches its highest intensity where humus is abundant. In some situations, such as boggy ground and clay, roots generally lack mycorrhizas, and in the case of transplanted seedlings mentioned above the association may be lost, indicating that the balance of interacting growth between fungus and root is quite susceptible to variations in the edaphic conditions.

When the circumstances are favourable, however, it is apparent that massed colonization of the root surface of germinating seedlings is a necessary preliminary stage in the course of mycorrhizal infection. Solitary mycorrhizal hyphae appear not to be able to penetrate the root epidermis.

The presence of sheets of mycelium along the radicle surface results in inhibition in growth of some emerging laterals, accompanied by a radial elongation of developing epidermal cells. Subsequent to this change in the epidermis, hyphae are able to effect intercellular penetration, and a mycorrhiza results. It is possible that inhibition and modification of root growth is due to secretions of auxin by the mycorrhizal fungus (Slankis, 1950: 40–44).

Lack of sufficient "inoculum potential" (Gar-

rett, 1956: 41) of the fungus, or a waning in the secretion of auxin, may account for the recovery from infection of some roots, which are then capable of bursting through the mantle and resuming extended growth.

SUMMARY

The root surface of germinating seedlings of *Nothofagus solandri* var. *cliffortioides* was found to be colonized at an early stage by superficial sheets of mycelium, but intracellular penetration was not apparent until the stage of emergence of lateral roots. Radial elongation of epidermal cells was always found to precede penetration by the mycorrhizal fungus. The presence of massed hyphae over the root-growing point appears to be necessary for the transformation of the root into a mycorrhiza.

ACKNOWLEDGMENTS

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Linear Discriminant Analysis

ROBERT H. RIFFENBURGH[1] and CHARLES W. CLUNIES-ROSS[2]

THE PROBLEM to be considered here is that of identifying, or of classifying, an observed individual as being a member of one of two "populations." This problem arises in some form in most sciences. A recent example is the problem, associated with certain international tensions, of classifying salmon caught in the North Pacific fishery as having arisen from the Asiatic or American salmon populations.

The populations are to be considered as giving rise to observable individuals each of which may be (partially) characterized by a set of k measurements. The measurements of individuals from either population are distributed as if they were independent observations on a multivariate distribution of probability. These distributions are assumed to be multivariate normal, with known parameters, for each population.

1. Statement of the Problem

When an individual is misclassified, there may or may not be loss functions associated with the misclassification. For the problems of this paper explicit results are not obtainable for general loss functions; we shall assume loss functions to be constants. Let us designate as α the loss associated with misclassification of an individual from population I and as β the loss associated with misclassification of an individual from population II; $\alpha, \beta > 0$. Also, there is the question of whether or not anything is known about the mixed population from which the individual to be classified is drawn; in particular, whether or not there are known a priori probabilities, under a random drawing, that an individual belongs to either of the parent populations. Let us designate the prior probabilities as p for population I and $q = 1 - p$ for population II.

It follows that there are four levels of the classificatory problem to be considered:

(1.1) (a) with loss functions and prior probabilities
(1.2) (b) with prior probabilities only
(1.3) (c) with loss functions only
(1.4) (d) with neither

Misclassifications are undesirable; however, there are no adequate common units in which the "undesirability" can be measured for all of the above levels. At each level there are two quantities for which some form of joint minimization is desired, viz.:

(1.5) (a) $\alpha p P_I$, $\beta q P_{II}$
(1.6) (b) pP_I, qP_{II}
(1.7) (c) αP_I, βP_{II}
(1.8) (d) P_I, P_{II}

where P_I is the probability that a random individual of population I is classified as having arisen from II, and P_{II} is the probability that a random individual of II is classified as having arisen from I.

These four pairs of quantities will be referred to indiscriminately as "error quantities."

Now either error quantity of a pair may be reduced to zero, but not both jointly. Thus, joint minimization of the error quantities is, to a certain extent, arbitrary. While various specifications of joint minimization can be formulated, the more reasonable are those which have already been proposed elsewhere in the literature, viz.:

(i) joint minimization may be specified as that which minimizes the sum of error quantities; let us denote this criterion as "minisum";
(ii) joint minimization may be specified as that which minimizes the larger of the error quantities; let us denote this criterion as "minimax."

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The first of these was introduced on level (a) by Brown (1950) and the second introduced on level (b) by Welch (1939). There has been more recent work on discriminant analysis, some of which is at levels similar to this treatment, but little seems applicable as the risk functions are not well defined.

Each of these specifications leads to the choice of one out of a family of quadratic discriminators. However, there are two related major difficulties: one is the determination of which member of the family is appropriate (for the minimax solution), and the other is that the integrals giving P_I and P_{II} cannot be evaluated explicitly (for either solution), and no tables are available for the resulting P_I and P_{II}.

If the variance-covariance matrices of the two populations are equal, the quadratic discriminator reduces to a linear discriminator; the integrals for P_I and P_{II} may then be reduced to the incomplete integral of the standard normal density. This is always true for any linear discriminator.

If we let A be a row vector of direction numbers, X be a row vector of variables (representing the possible measurements on the individual), c be a constant, and let primes denote transposition, then a linear discriminator may be written:

$$AX' = c. \qquad (1.9)$$

We lose no generality if we number the populations such that the individual represented by X is classified into population I if $AX' < c$ and into population II if $AX' \geqslant c$.

Let (m_1, σ_1^2), (m_2, σ_2^2) be the mean and variance of AX' when X is distributed as in populations I, II, respectively. Then it follows, using an obvious notation, that:

$$P_I = \int_{-\infty}^{\frac{c-m_1}{\sigma_1}} f(u)\,du$$

$$P_{II} = \int_{\frac{c-m_2}{\sigma_2}}^{\infty} f(u)\,du$$

2. *The Appropriate Linear Function*

For the case when the distributions have identical variance-covariance matrices, the vector A is well known (see, for example, Fisher, 1936), being the inverse of this common matrix multiplied by the vector of difference means. When the variance-covariance matrices are not equal but are proportionate, then the corresponding A (using either of the matrices) is still optimum under both the minisum and minimax criteria.

In many fields the assumption of proportionate but not necessarily equal variance-covariance matrices is not unreasonable. This situation occurs, for example, in marine biology. The Hawaiian tunas *ahi* (*Neothunnus macropterus*) and *ahipahala* (*Thunnus alalunga*) are similar in most respects, but the *ahi* is a larger and more complex fish. If weight, fork length, lengths of second dorsal and anal fins, and the ratio of the length of the pectoral fin to the fork length (which varies inversely as the first four variables) are taken to be the variables, the population variance-covariance matrices for the *ahi* and *ahipahala* are (expected to be) proportional but unequal. Another example is cited in the literature, although only two variables were used. Mottley (1941) found that the variances and covariance for head and body measurements of trout (*Salmo gairdnerii kamloops*) stocked in two Canadian lakes were proportional.

The optimum A for general dispersion matrices is not easy to derive. This problem is considered in another paper by the authors (1960). The current paper considers optimum c for given A and thus in what follows it is only necessary to consider that A has been determined either by the methods mentioned above or arbitrarily.

3. *The Constant c for Minimized Error Quantities*

We lose no generality if we let $m_2 > m_1$ and $\sigma_2 \geqslant \sigma_1$. The designation of the population having the larger standard deviation as population II is arbitrary. We may then make a scale transformation of ± 1, whichever is necessary to obtain $m_2 > m_1$.

We now wish to obtain expressions for the constant c which will minimize the error quantities under the minisum and minimax criteria, respectively.

Consider $\alpha p P_I + \beta q P_{II}$.

$$\frac{\partial}{\partial c}\left[\alpha p P_I + \beta q P_{II}\right] = \frac{\alpha}{\sqrt{2\pi}\sigma_1}\exp\left\{-\frac{1}{2}\left(\frac{c-m_1}{\sigma_1}\right)^2\right\} - \frac{\beta}{\sqrt{2\pi}\sigma_2}\exp\left\{-\frac{1}{2}\left(\frac{c-m_2}{\sigma_2}\right)^2\right\}$$

Equating the derivative to zero and rearranging, we obtain

$$\ln\frac{\beta\sigma_1}{\alpha\sigma_2} = \left(\frac{c-m_1}{\sigma_1}\right)^2 - \left(\frac{c-m_2}{\sigma_2}\right)^2$$

which is a quadratic in c with minisum c as roots:

$$c(\text{minsum}) = \frac{1}{\sigma_2^2-\sigma_1^2}\left\{\sigma_2^2 m_1 - \sigma_1^2 m_2 \pm \sigma_1\sigma_2\left[(m_2-m_1)^2 + (\sigma_2^2-\sigma_1^2)\ln\frac{\alpha^2\sigma_2^2}{\beta^2\sigma_1^2}\right]^{\frac{1}{2}}\right\}$$

Equation (3.3) has three possibilities:

(1) when there are no real roots,
(2) when no roots fall in (m_1,m_2), and
(3) when one and only one root falls in (m_1,m_2).

If a root should fall at one of m_1,m_2, this may be considered as a limiting case of situation (2). Situation (1) is trivial; all individuals are classified into one population. In situation (2), linear discrimination is not very helpful; quadratic discrimination is indicated. In these situations, possibly (depending on parameters) there is no discrimination which will be much of an improvement over the classification of all individuals into one population or a purely random classification. Thus, situation (3) will be considered in this paper.

When a root falls in (m_1,m_2), this is the root which minimizes $\alpha p P_I + \beta q P_{II}$, and is therefore the root desired. The other root maximizes $\alpha p P_I + \beta q P_{II}$ and therefore will not be used. Since σ_2 has been arranged to be greater than σ_1, and the smaller root is less than m_1, the positive square root is required. When $\sigma_1 = \sigma_2$, c(ms) is the root in (m_1,m_2); the other root is infinite.

Consider now the minimizing max $(\alpha p P_I, \beta q P_{II})$. $\alpha p P_I$ and $\beta q P_{II}$ are monotonic, decreasing and increasing respectively, in c; and, therefore, the desired c is located such that $\alpha p P_I = \beta q P_{II}$. An explicit result will not be found in general, since the integrals have not been evaluated explicitly. If $\alpha p = \beta q$, we have the integrals identical except for upper limits of integration, and $\alpha p P_I = \beta q P_{II}$ reduces to

$$\frac{c-m_1}{\sigma_1} = \frac{c-m_2}{\sigma_2}$$

Solving, we obtain a minimax c:

$$c(\text{mmx}) = \frac{m_1\sigma_2 + m_2\sigma_1}{\sigma_2+\sigma_1}$$

It should be noted that if $\sigma_1 = \sigma_2$ and $\alpha p = \beta q$, both c(ms) and c(mx) reduce to a c dependent upon only the centroids,

$$c(m) = \frac{m_1+m_2}{2}$$

This c(m) is the population analogue of the c introduced for samples by Barnard (1935) and Fisher (1936) and currently used in linear discriminant analysis.

4. A Discussion of Levels and c's

The results (3.3) and (3.5) apply for the case in which loss functions and prior probabilities are known, i.e., (1.1). When either or both of these quantities are unknown, corresponding to (1.2), (1.3), or (1.4), the corresponding error quantities considered are given by (1.6), (1.7), or (1.8) respectively. The results corresponding to (3.3) and (3.5) are obtained readily by the following substitutions in (3.3) and (3.5):

(1.2) "prior probabilities only": $\alpha = \beta = 1$
(1.3) "loss functions only": $p = q = 1$
(1.4) "neither": $\alpha = \beta = p = q = 1$.

For level (a), where both prior probabilities and loss functions are known, the risk may be measured and specified. If the total risk is to be minimized, then c(ms) is the appropriate constant. If the risk is to be minimized, subject to the restriction that risks from each source are to be equal, then c(mx) is the appropriate constant.

For level (b), where prior probabilities only are known, then c(ms) minimizes the conditional probability of misclassification. However, if classification is only part of the problem at

hand, then it may be desirable, in order to avoid bias in later stages, say, to minimize, subject to equalizing the probabilities of the two types of misclassification; here c(mx) is the appropriate constant.

For example, consider a merchandizing situation. If the problem is to allocate a limited shipment of goods to two branches of the same store, the same management suffers the loss from understocking either branch, and c(ms) is the appropriate constant to use in specifying the quantities of goods to go to each branch. On the other hand, if the problem is to equalize buyer-seller risk, as in the case of an independent mediator handling quality control, then c(mx) is the appropriate constant to use in specifying the acceptable level of quality.

For levels (c) and (d), the error quantities are in no sense absolute quantities. Here c(mx) will be the most reasonable constant to use, since under the minimax solution the expected numbers of misclassifications are equal for the two populations.

In practice, α, β, p, and q may or may not be well defined conceptually, but either way will often, perhaps usually, be unknown. Thus a comparison between discriminators using c(ms), c(mx), and c(m) at level (d) is appropriate.

5. *Comparison of Discriminators*

Introduction. The discriminators may be compared on the basis of our minisum and minimax criteria. Let us designate these criteria respectively in terms of the error quantities as

(i) $P_s = P_I + P_{II}$
(ii) $P_x = \max(P_I, P_{II})$.

In comparing discriminators, it can happen that either one has both criteria less than or equal to those of the other or this does not occur. If the former holds, then the discriminator with the smaller criteria may be said to be better than the other. This is true whether the discrimination is linear or not.

For the purposes of this paper, A has been taken to be a vector of constants. Thus, while linear discriminators are functions of both A and c, our comparison need be concerned only with varying c's. The restriction to level (d) together with the vector of constants, A, enables us to keep the number of parameters down to two for comparisons of the discriminators $AX' = c(ms)$, $AX' = c(mx)$, and $AX' = c(m)$. c(ms) and c(mx) are the c's derived for the two criteria; both reduce to c(m) in the special case of equal dispersion matrices. c(m) is the population analogue of the c used in practice and is easier to compute than are c(ms) and c(mx). Since c(mx) and c(ms) each minimize one criterion, the comparisons will be to find the conditions under which c(m) leads to both smaller P_s than does c(ms) and smaller P_x than does c(mx). When these conditions are satisfied then c(m) may be regarded as a compromise between c(ms) and c(mx).

The two essential parameters will be defined as

(5.1) $B = \sigma_2^2/\sigma_1^2$

(5.2) $C = \frac{m_2 - m_1}{\sigma_2^2 - \sigma_1^2}$

It can be seen that $B \geq 1$ and $C > 0$. If results in B and C should be tabulated, the tables would be symmetric in log B, — log B, and in C, — C.

Condition for reasonable linear discrimination. Under certain conditions, linear discrimination does not yield good results; an example of this is the situation in which the centroids of the two populations are the same. Any description of the conditions necessary for linear discrimination to be able to lead to reasonable results must be, to some extent, arbitrary. Generally, the situations in which linear discrimination may be rejected are typified by no root of c(ms) being contained in (m_1, m_2).

At level (d) there are always two real solutions of (3.3). By restricting our interest to the range (m_1, m_2) it follows from considerations of monotonicity, continuity, and limiting behavior that a necessary and sufficient condition for the existence of a root of (3.3) in this range is

(5.3) $\frac{1}{\sigma_1\sqrt{2\pi}} \exp\left\{-\frac{1}{2}\left(\frac{c-m_1}{\sigma_1}\right)^2\right\} > \frac{1}{\sigma_2\sqrt{2\pi}}$

since the left and right sides of the inequality are the densities of populations I and II at m_2. (5.3) may be rewritten in terms of B and C as follows:

(5.4) $c^2 - 2c(m_2 - Bm_1)/(1-B) > \ln B$

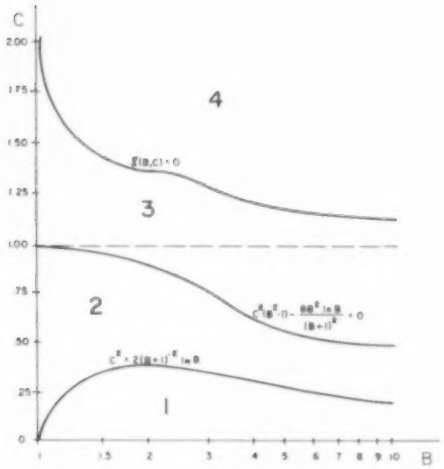


FIG. 1. Four regions in (B, C) corresponding to the properties: (1) no linear discriminator reasonable; (2) $c(m)$ is a compromise between $c(ms)$, $c(mx)$; (3) $c(ms)$ is better than $c(m)$; (4) both $c(mx)$, $c(ms)$ are better than $c(m)$. In general, the larger the C, the stronger will be the discriminator.

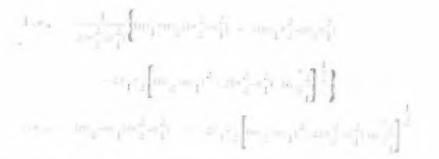
The lower curve in Figure 1 separates the regions in (B, C) for which (5.4) is true, untrue. Thus in region 1 a quadratic discriminator is appropriate; elsewhere a linear discriminator is appropriate.

Investigation of when c(ms) is better than c(m). Let us denote the larger conditional probability of misclassification, P_s, using c(m), c(ms) by $P_s(m)$, $P_s(ms)$ respectively.

Now c(mx) is the point on either side of which the probabilities of misclassification are equal, so that a $c < c(mx)$ indicates $P_I = P_s$ and a $c > c(mx)$ indicates $P_{II} = P_s$. Further, $m_2 \geqslant m_1$, $\sigma_2 \geqslant \sigma_1$ imply that both c(m) and c(ms) are greater than c(mx) since:

Therefore, $P_s(m) = P_{II}(m)$ and $P_s(ms) = P_{II}(ms)$.

It follows immediately that a necessary and sufficient condition for $P_s(m) > P_s(ms)$ is $c(m) > c(ms)$,



which may be rewritten as:

The center curve in Figure 1 separates the regions of (B, C) for which P_s using $AX' = c(ms)$ is greater, less than those using $AX' = c(m)$. Thus in regions 1 and 2, c(m) is better with respect to the minimax criterion; in regions 3 and 4, c(ms) is better with respect to the minimax criterion.

Investigation of when c(mx) is better than c(m). Let us denote the sum of conditional probabilities of misclassification, P_s, using c(m), c(mx) by $P_s(m)$, $P_s(mx)$.

On expressing P_I, P_{II} in terms of c(m), c(mx) and hence in terms of B, C, it follows, after rearrangement, that

say. From differential-geometrical considerations and the fact that both c(m), c(ms) are greater than c(mx), it follows that $c(m) < c(ms)$ implies that $P_s(m) < P_s(mx)$. The upper curve in Figure 1 is the curve $g(B, C) = 0$, which separates the regions of (B, C) for which the sum of conditional probabilities of misclassification using $AX' = c(mx)$ is greater, less than those using $AX' = c(m)$. Thus in region 4, c(mx) is better with respect to the minisum criterion; elsewhere c(m) is better with respect to the minisum criterion. The asymptote as B tends to infinity is, approximately, $C = 1.029$.

Figure 2 shows g(B, C) plotted against C for several values of B.

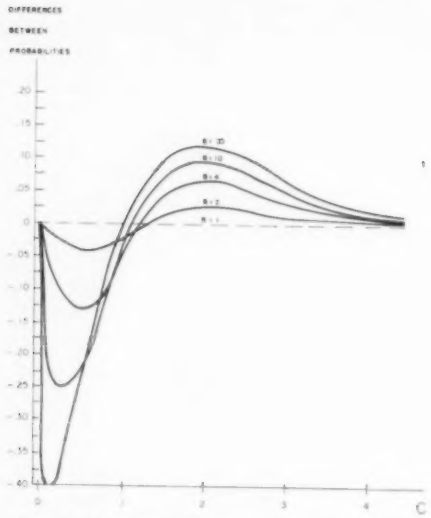


FIG. 2. Difference between (a) the sum of conditional probabilities of misclassification using $c(m)$, and (b) the same using $c(mx)$, expressed as a function of C for several values of B.

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Albacore Migration and Growth in the North Pacific Ocean as Estimated from Tag Recoveries

TAMIO OTSU[1]

THE ALBACORE, *Germo alalunga* (Bonnaterre), is considered a choice tuna by Americans because of its excellent canning quality. It is fished by Americans along the Pacific coast of the United States and by the Japanese in North Pacific waters extending from the coast of Japan to about the 180th meridian. In recent years the Japanese have extended their albacore fishing grounds to tropical and subtropical waters of the Pacific and Indian oceans (Mimura, 1957; Van Campen[2]), and more recently, to Atlantic waters.

A tagging program was instituted by the Pacific Oceanic Fishery Investigations (POFI) [in 1959 it became the Bureau of Commercial Fisheries, Hawaii Area] as a part of an albacore research project being conducted under Public Laws 329 (80th Congress) and 466 (Saltonstall–Kennedy Act, 83rd Congress). Employing the California type-G "spaghetti" tag (Wilson, 1953) (Fig. 1), and to a limited extent, the POFI- developed dart tag (Yamashita and Waldron, 1958), tagging was conducted on albacore taken by POFI vessels on exploratory cruises to the North Pacific. Intensive albacore tagging has been conducted on the West Coast by the California Department of Fish and Game and data on some of their recoveries have been published (Blunt, 1954; Ganssle and Clemens, 1953). This report summarizes the tagging results obtained by POFI, and includes a preliminary analysis of albacore migration and growth.

ACKNOWLEDGMENTS

The success of a tagging program depends largely on the cooperation of the fishermen making the recoveries, their interest in the program, and the care with which they record and transmit data pertinent to each recovery. We extend our gratitude to the numerous commercial fishermen and research agencies, both in the United States and in Japan, who have rendered excellent cooperation in this respect.

The writer is indebted to Dr. Robert H. Riffenburgh of the University of Hawaii for guidance in the growth analysis.

ALBACORE TAG RELEASES

Between January, 1954, and August, 1957, a total of 1,201 albacore was tagged and released in the temperate North Pacific (Fig. 2). Included in the total are 270 albacore tagged in the Japanese live-bait fishing grounds in the spring of 1956 (Van Campen and Murphy, 1957). The remaining tag releases were made in the central and eastern North Pacific, and consisted of 855 fish taken by surface trolling and 76 taken by long-lining.

The size-frequency distribution of the tagged albacore is given in Figure 3. The 270 fish tagged off Japan are not included since they were not measured. Measurements were made, however, on samples of fish from each school in which tagging was conducted, and these indicated a relatively narrow size range of 60.4 cm. to 83.4 cm. in length. In addition to these, 94 troll-caught fish tagged off the California coast are not included since no measurements were recorded. The long-line gear accounted for a wide size range of fish (50 to 120 cm.) while surface trolling took fish up to 87 cm. in length (Fig. 3).

ALBACORE TAG RECOVERIES

As of September, 1958, 15 (1.2 per cent) of POFI's tag releases had been recovered (Table 1). Seven of the recoveries (Nos. 1, 2, 3, 8, 9,

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[2] Van Campen, W. G. MS. The Japanese summer albacore fishery. Submitted for publication as a research report.

TABLE 1
POFI ALBACORE TAG RECOVERIES

NO.	DATE TAGGED	POSITION OF RELEASE		DATE RECAP-TURED	POSITION OF RECAPTURE		NET DISTANCE TRAVELLED (miles)	DAYS OUT
		Latitude	Longitude		Latitude	Longitude		
1	10/4/54	46° 30′ N.	159° 18′ W.	11/28/55	35° 45′ N.	157° 39′ E.	2,055	420
2	10/5/54	43° 31′ N.	161° 16′ W.	1/19/56	35° 23′ N.	141° 20′ E.	2,670	471
3	10/9/55	42° 16′ N.	147° 16′ W.	6/24/56	31° 54′ N.	158° 37′ E.	2,660	259
4	10/17/55	44° 55′ N.	144° 48′ W.	8/1/56	31° 21′ N.	117° 17′ W.	1,515	288
5	7/31/56	44° 31′ N.	174° 55′ W.	7/23/57	30° 08′ N.	119° 03′ W.	2,775	357
6	8/1/57	34° 49′ N.	121° 57′ W.	9/17/57	34° 49′ N.	121° 26′ W.	26	47
7	7/22/57	35° 43′ N.	122° 58′ W.	10/7/57	36° 24′ N.	123° 07′ W.	41	77
8	10/16/55	43° 40′ N.	144° 40′ W.	11/23/57	33° 22′ N.	174° 07′ E.	2,025	769
9	11/17/56	36° 44′ N.	127° 37′ W.	11/17/57	38° 08′ N.	174° 53′ E.	2,800	365
10	7/23/57	42° 20′ N.	127° 33′ W.	5/26/58	32° 15′ N.	144° 15′ E.	4,230	287
11*	7/22/57	47° 00′ N.	126° 18′ W.	6/10/58	33° 40′ N.	144° 00′ E.	4,300	323
12	7/16/57	44° 47′ N.	130° 04′ W.	7/11/58	30° 00′ N.†	118° 45′ W.†	1,035	360
13	7/16/57	44° 47′ N.	130° 04′ W.	8/22/58	32° 00′ N.†	122° 00′ W.†	860	402
14	11/14/56	38° 00′ N.	128° 25′ W.	8/23/58	32° 15′ N.	122° 30′ W.	455	647
15	11/21/56	35° 21′ N.	123° 57′ W.	7/21/58	34° 00′ N.	122° 10′ W.	130	607

* Fish No. 11 was marked with a POFI dart tag; all others with California "spaghetti" tags.
† Approximate position of recapture.

10, 11) were made by the Japanese in their summer live-bait and winter long-line fisheries, while the remaining 8 were made by Americans in the West Coast fishery.

With the exception of two American recoveries (Nos. 6 and 7) which were made within 47 and 77 days, respectively, of the date of release, the remaining 13 represented relatively long periods between release and recovery, ranging from 259 to 769 days. While all of these long-term recoveries provided valuable information on the movements of albacore in the North Pacific, complete data on growth were not obtained since information on several of the recoveries did not include length or weight measurements.

FIG. 1. An albacore (recovery No. 4) with a California type-G tag attached. This fish was at liberty for approximately 10 months before recapture (Table 1).

MOVEMENTS SHOWN BY TAGGED ALBACORE

The net movements of the tagged fish are depicted in Figure 4. Perhaps most significant is the migration of fish between the major fisheries. A fish tagged in the American fishery off California (No. 9) moved across into the Japanese mid-ocean winter long-line grounds to be retaken there. Two others tagged in the West Coast fishery off the Pacific northwest (Nos. 10, 11) made a complete trans-Pacific migration and were recaptured in the Japanese live-bait fishery. Albacore tagged in mid-ocean north of Hawaii migrated into the West Coast fishery (Nos. 4, 5) as well as into the Japanese long-line (Nos. 1, 2, 8) and live-bait (No. 3) fisheries. Tag recoveries reported by the California Department of Fish and Game also showed movements of albacore from waters off California to the coast of Japan (Ganssle and Clemens, 1953). Movement in the opposite direction, from the Japanese fishery into the American fishery, has yet to be demonstrated.

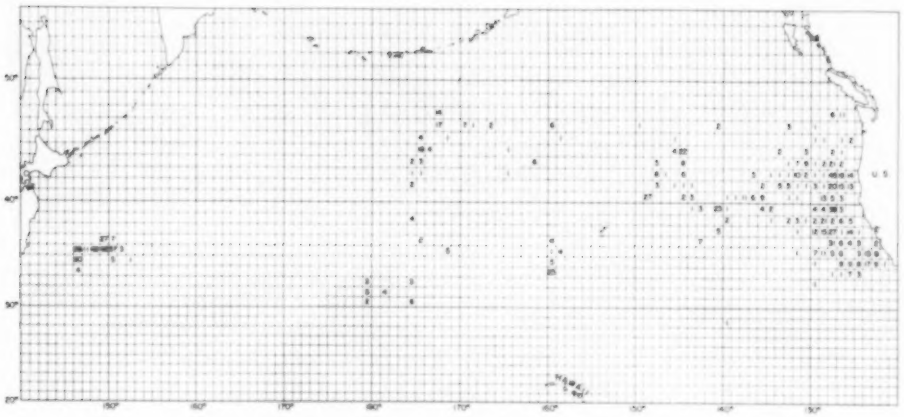

Fig. 2. Numbers and locations of POFI tag releases, January, 1954–August, 1957. (California type-G tag was used on 1,090, and the POFI dart tag on 111 albacore.)

GROWTH SHOWN BY THE TAGGED ALBACORE

Of 15 recoveries to date, 11 were accompanied by size data at the time of recovery (Table 2). The estimated annual growth of these fish was extremely variable, ranging from 3.8 to 28.7 cm. per year.

Although it is realized that the available data are inadequate for any conclusive growth study, a preliminary analysis was made in order to present some approximation of the albacore growth rate. Following the method of growth curve transformation described by Walford (1946), the length of fish at the time of release (age N) was plotted against the length after one year (age $N + 1$), the latter representing the length at release plus the estimated value of one year's growth (Fig. 5). There is a suggestion of linearity in the plots, with the exception of one (No. 2, Table 2). The growth reported for this fish is obviously out of proportion to the others. When the Japanese transmit data pertinent to a tag recovery they usually specify the method of measurement used. This was not done in this particular instance; for this reason and because the reported length seems excessive, this fish is dropped from further consideration. The remaining 12 points (including two from published California data) fall about the regression line $Y = 26.29 + .77867X$ obtained by the least squares method, where Y is the length at $N + 1$, and X the length at N.

Also shown in Figure 5 is the line of no growth ($L_N = L_{N+1}$) drawn in with a 45° slope through the origin. The point of intersection between the regression line and the line of no growth is described by Walford as the upper asymptote of the growth curve, which in this case falls at approximately 118 cm. The 118-cm. asymptote of maximum growth for the sample data of this paper is slightly less than that which would be expected for albacore populations in general; measurements of commercial landings indicate the population asymptote to be about 124 cm. (Suda, 1954; Otsu and Uchida, 1959*a*).

The growth curve (Fig. 6) was derived from Figure 5. This method does not enable us to obtain that portion of the growth curve falling below the point of inflection, and since the smallest fish for which there are data is a 60-cm. fish, the extrapolation toward the smaller sizes is dubious.

In an attempt to describe the complete growth curve, particularly that portion falling below the point of inflection, for which Walford's method does not apply, the data were fitted to a Gompertz equation, $y = ab^{-e^{-kx}}$, where y is the length in centimeters and x the age in years. A

TABLE 2
GROWTH SHOWN BY TAGGED ALBACORE

NO.	DATE OF RELEASE	DATE OF RECOVERY	DAYS OUT	SIZE AT RELEASE (cm.)	SIZE AT RECOVERY (cm.)	NET GAIN (cm.)	GAIN PER YEAR (cm.)
1	10/4/54	11/28/55	420	78.2	—	—	—
2	10/5/54	1/19/56	471	68.0	105.0	37.0	28.7
3	10/9/55	6/24/56	259	63.4	—	—	—
4	10/17/55	8/1/56	288	59.9	72.3	12.4	15.7
5	7/31/56	7/23/57	357	68.4	78.0	9.6	9.8
6	8/1/57	9/17/57	47	66.5	—	—	—
7	7/22/57	10/7/57	77	65.5	67.0	1.5	7.1
8	10/16/55	11/23/57	769	65.1	94.8	29.7	14.1
9	11/17/56	11/17/57	365	85.2	97.5	12.3	12.3
10	7/23/57	5/26/58	287	78.0	85.2	7.2	9.2
11	7/22/57	6/10/58	323	75.0	—	—	—
12	7/16/57	7/11/58	360	65.0	77.3	12.3	12.5
13	7/16/57	8/22/58	402	75.0	84.5	9.5	8.6
14	11/14/56	8/23/58	647	79.4	92.6	13.2	7.4
15	11/21/56	7/21/58	607	68.6	86.4	17.8	10.7
A*	8/11/53	2/2/54	176	84.0	88.0	4.0	8.3
B*	8/16/53	2/23/54	192	91.0	93.0	2.0	3.8

* Fish tagged by the California Department of Fish and Game and reported by Blunt (1954).

rapid approximation method by Riffenburgh[3] for estimating the parameters of the Gompertz curve was used. The same paper contains a lengthier and more precise method in which the estimates converge stochastically to the parameters, but it was felt that the number of data available was inadequate to assure convergence. Thus, the approximation technique was utilized.

The method uses three sets of data points: $(i,\ y_i)$, $(i+j,\ y_{i+j})$, and $(i+k,\ y_{i+k})$. The numerical calculation involved is markedly simplified if $k = 2j$. In this case, the triplet of points having x-values of $N + 3$, $N + 5$, and $N + 7$ (Fig. 6) was selected from among the set of triplets possessing the property $k = 2j$; these points fall approximately within the portion of the curve for which there are observed data. The corresponding y-values, obtained from Walford's curve, were $y_3 = 62.7$ cm., $y_5 = 84.8$ cm., and $y_7 = 98.2$ cm. The estimate of the parameter $c = 1.43$ was obtained by the equation:

$$c^{-j} = \frac{\log \dfrac{y_{i+k}}{y_{i+j}}}{\log \dfrac{y_{i+j}}{y_i}}$$

and the estimate of the parameter $b = 0.177$ by the equation:

$$\log b = \frac{\log \dfrac{y_{i+k}}{y_{i+j}}}{c^{-i}\, c^{-j}\, (c^{-j-1})}.$$

[3] Riffenburgh, R. H. MS. A new method for estimating parameters of the Gompertz growth curve. University of Hawaii and Pacific Oceanic Fishery Investigation, U. S. Fish and Wildlife Service, Honolulu.

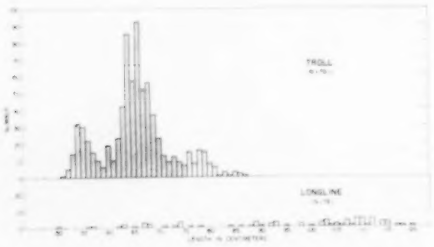

FIG. 3. Size-frequency distribution of albacore tagged by POFI in the North Pacific, January, 1954–August, 1957.

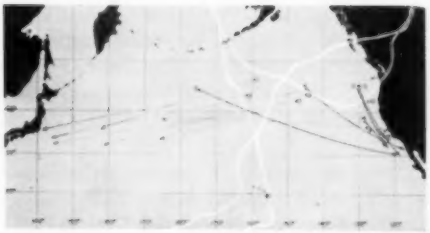

FIG. 4. Net movements of albacore tagged by POFI. (The lines have no significance other than connecting the points of release and recovery of each fish.)

The parameter a, or the upper asymptote of the growth curve (118 cm.), had already been estimated by Walford's method. These parameters were fitted into the Gompertz equation as follows:

$$y = (118)\ (0.177)^{(1.43)^{-x+d}}$$

which resulted in the asymmetric sigmoid curve shown in Figure 7. Inspection showed that if this curve is shifted 0.23 year to the right, it will present an adequate fit for the data; thus, an estimate of d is 0.23.

The curve derived by the Walford method (Fig. 6) is superimposed on the Gompertz curve. There is fair agreement between the two in the portions representing lengths between 40 and 85 cm., and the observed data do not deviate much from either curve. If albacore growth follows a typical Gompertz curve, then this represents a possible entire growth curve of the albacore, including that portion not possible to determine by the Walford method. It should now be possible to assign specific ages.

It can be seen by inspection that the curve approaches the abscissa reasonably closely at N — 2 years, suggesting that hatching is in this time vicinity. While the size indicated at hatching deviates from the expected size to the order of 2 cm., this error is not large considering the assumedly random deviations of the observed data from the estimated growth curve and the small sample size. With N — 2 as the arbitrary origin, the adjusted ages are given below the original designations. The resulting length for each year beginning with this origin is presented in Table 3 along with values obtained by the Walford method. While there is every indication that at least a portion of each curve reliably represents the albacore growth, those portions for which there are no observed data should be considered tentative. The initial growth by the Gompertz curve appears to be unreasonably slow since it requires about 3 years for a fish to attain a weight of 1 pound (about 30 cm.). The early growth is slow, relative to the result obtained by the Walford method. The results suggest a possible error in assigned ages of 1 or 2 years.

This disagreement and others may result from one or a combination of the following debilities: (a) the assumption that albacore growth follows the Gompertz curve may be unwarranted; (b) the number of observations may be inadequate; (c) there is the possibility that there is differential growth between the sexes after the onset of sexual maturity, causing an unbalanced sex ratio in favor of males among the larger albacore (Otsu and Uchida, 1959*b*). If this is true, then the growth curves are subject to inaccuracies in the upper portions representing fish larger than 90 cm., the approximate size at which the albacore is believed to attain sexual maturity. A differential growth rate may have been responsible for the slightly

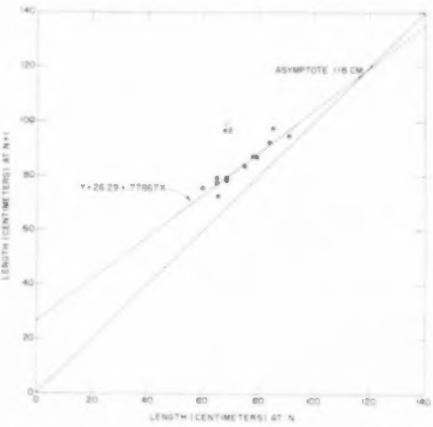

FIG. 5. Growth shown by tagged fish plotted by Walford's (1946) method and fitted with a straight line. The intersection of this line and the line $L_n = L_{n+1}$ indicates the upper asymptote of the albacore's length. Fish No. 2 was excluded from calculation of the regression line.

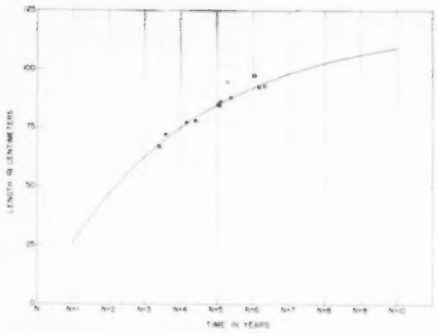

FIG. 6. Portion of growth curve of albacore obtained by Walford's method. Observed data are superimposed.

low estimate of the upper asymptote (Fig. 5) and for the deviation of the observed data from the upper portions of both curves (Figs. 6, 7).

Some studies have been made in the past on the age and growth of albacore, such as those by Uno (1936*a*; 1936*b*), Aikawa and Kato (1938), Partlo (1955), and Figueras (1955), all of which were based on the vertebral method of age estimation. Otsu and Uchida (1959*b*) also attempted to determine the age of albacore by this method and concluded in their study that the rings found on the centrum are probably not annuli as assumed by the several workers, but rather are growth marks laid down randomly with respect to time, and that, therefore, aging could not be accomplished by this method. In addition, they thought that the vertebral method generally yielded growth curves that were too linear to be typical and growth rates that were too slow when compared with the evidence from the then meager tag returns. The results of this study substantiate their criticisms.

The growth curves in question are compared with the curve obtained in this study (Fig. 8). Since the ages assigned in this paper (Fig. 7, Table 3) were arbitrarily defined, and since there are obvious discrepancies in the ages assigned by various workers, the mean lengths are plotted at yearly intervals without regard to the specific ages given. In other words, the curves in Figure 8 may be shifted freely in either direction along the abscissa. It is noted that the several growth rates do not differ markedly in magnitude.

It is clearly seen, however, that the presently derived curve, at least a portion of which is believed to be a fair representation of the actual albacore growth curve, is curvilinear, while the others, with the possible exception of Uno's (1936*b*) results, are almost perfectly linear. This difference in curvature supports the contention that the age of albacore could not be determined by the vertebral method. The linearity suggests that the rings found on the vertebrae are associated with growth rather than with age, and that ring formation is a linear function of fish growth.

Aside from growth studies by the vertebral

TABLE 3

GROWTH RATES OF ALBACORE DERIVED BY FITTING TAG RECOVERY DATA TO GROWTH CURVES BY THE METHODS OF WALFORD AND RIFFENBURGH

AGE* (years)	LENGTH (cm.)	
	Walford	Riffenburgh
1	—	7.5
2	—	17.3
3	26.3	31.5
4	46.8	46.5
5	62.7	62.5
6	75.1	75.0
7	84.8	86.0
8	92.3	94.5
9	98.2	101.0
10	102.7	106.0

* The ages given are based on an arbitrarily selected origin (Fig. 7) and are therefore tentative.

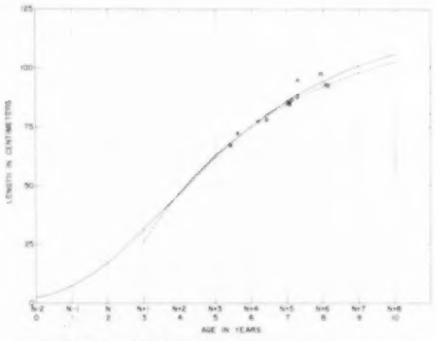

FIG. 7. Growth data fitted to a Gompertz equation by Riffenburgh's short method. The curve obtained by Walford's method (dashed) is superimposed. Observed data are superimposed on the Gompertz curve.

method, several workers have analyzed albacore size frequencies. Brock (1943) found two regularly occurring modal groups in the California length frequencies for the years 1924 to 1928 inclusive. The consistency in the appearance of these groups indicated that they were year classes. A more uniform relation was seen in the "lagged difference," or the difference in the modal size of group A in 1 year with that of group B in the following year, rather than between the two modal groups of the same year. The modal lengths (lagged) of both California and Oregon albacore are reproduced in Table 4.

The lagged modal values for the California albacore fall in nearly perfect agreement with the growth shown by the tagged fish, indicating that the distinctly bimodal distribution represents two age groups, one a year older than the other, as postulated by Brock. The growth of the Oregon albacore, on the other hand, was somewhat less than that estimated for the California albacore, and consequently lower than the growth shown by the tagged fish.

Suda (1954) has examined the size distribution of albacore taken in the Japanese winter long-line season and has traced six different size groups which appear yearly. The modes of these groups were: 57 cm., 67 cm., 78 cm., 89 cm., 100 cm., and 111 cm. The spacing of the intervals is uniformly 10 or 11 cm., thus representing a straight-line growth if these length groups are assumed to be age classes. The author concluded that these length groups may be considered as age groups if they are handled as five groups consisting of ages I to IV and an advanced age group which includes the last two modal groups. If these modal lengths are compared with the results obtained from tagging, it is seen that as in the case of the results obtained by the vertebral method, the yearly growth increments do not differ greatly, but there is a marked difference in the curvatures of the two curves. Suda pointed out that since growth of most living organisms is logistic, it may be unreasonable to postulate these length groups as age groups. However, he advanced the possibility that these age groups fall within the relatively straight portion of the growth curve. This is not indicated by the data presented in this paper.

TABLE 4
MODAL LENGTHS OF CALIFORNIA AND OREGON ALBACORE, IN CENTIMETERS
(Reproduced from Table 7, Brock, 1943)

GROUP A	GROUP B	DIFFERENCE
CALIFORNIA ALBACORE (1924 to 1928)		
1924, 64.89	1925, 77.18	12.29
1925, 64.87	1926, 77.16	13.29
1926, 68.84	1927, 81.04	12.20
1927, 65.80	1928, 78.27	12.47
OREGON ALBACORE (1938 to 1940)		
1938, 66.18*	1939, 74.19	8.01
1939, 64.02	1940, 74.26	10.24

* Only a single small sample was taken in 1938 after the season was underway.

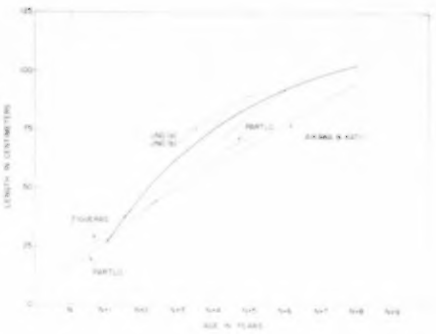

FIG. 8. A comparison of the growth curves obtained by the vertebral method with the Walford curve obtained in this study. Specific ages are disregarded in the plotting of these curves.

DISCUSSION

The tag recoveries have shown that albacore migrate considerable distances, and from one fishery to another, suggesting that there is a single population of albacore in the temperate North Pacific, exploited seasonally by Americans off the West Coast during the summer and fall, by the Japanese in mid-ocean during the winter, and also by the Japanese in the western Pacific during the spring and summer.

While no recoveries of albacore tagged off Japan have yet been reported in the American fishery, there are suggestions of movements in that direction. For example, recoveries 11 and 12 were of fish tagged within a week of each

other in waters of the American fishery off the Pacific northwest. One was recaptured in June, 1958, in the Japanese live-bait fishery, and the other, a month later in the American fishery. The suggestion is that the latter had also undergone an extensive migration to the west before returning to the American fishery, although this movement may not have been as complete as the other. A similar suggestion is made by the recapture in the American fishery after 306 days of an albacore tagged by the California Department of Fish and Game. One other albacore, tagged at the same time, had been recaptured a month earlier 145 miles east of Tokyo, Japan (Anonymous, 1957). An appreciable tagging program by the Japanese may show definitely whether or not there is a movement of fish from the Japanese live-bait fishery into the American fishery.

However, judging by the sizes of fish generally taken in the different fisheries, it is possible that even extensive tagging by the Japanese would not confirm such a movement towards the east. The chances for American recovery of Japanese-tagged fish are not good unless the Japanese tag unusually small fish or unless unusually large fish move into the American fishery in large numbers. The sizes of fish commonly taken in the respective fisheries are shown in Figure 9. The American West Coast fishery generally takes smaller albacore than either the Japanese live-bait fishery or their long-line fishery; the fish range in size from about 50 to 85 cm. with the predominant sizes around 65 cm. The bulk of the fish taken by the Japanese is larger than 70 cm. in length, and these sizes comprise only a very small part of the American landings. On the other hand, small albacore under 70 cm. may be present in larger numbers in the Japanese live-bait fishery than indicated in Figure 9. Suda (1955) states that such small fish constitute a significant portion of the landings during certain years. The chances for recovery would seemingly be improved if tagging is concentrated on such small fish.

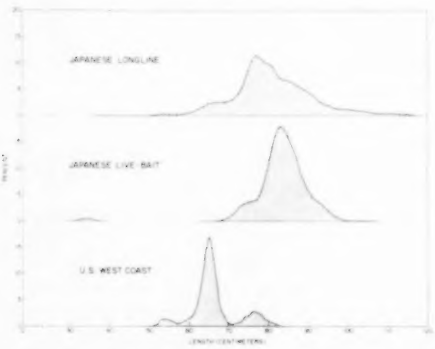

FIG. 9. Examples of albacore sizes taken by the major North Pacific fisheries. The Japanese size-frequencies were obtained from Nankai Regional Fisheries Research Laboratory (1951). The West Coast length frequency is based on unpublished data of the Oregon Fish Commission and are measurements made on albacore landed in Oregon during the 1957 season.

Although there appears to be little chance for fish tagged in the western Pacific to be recovered in the American fishery, a large-scale tagging program by the Japanese stands to serve an equally important purpose, that of elucidating the relationship between the albacore of the temperate and tropical Pacific Ocean. There is at present no direct knowledge concerning the movements of the larger albacore. The larger fish of the temperate North Pacific appear to move south into tropical and subtropical waters, perhaps to form the reproductive segment of the population. If there is such a southward migration of the larger fish, this may be shown someday by the recovery of a tagged fish. With Japanese vessels exploiting wide areas in the tropical Pacific, chances for recovery of fish tagged in the north should be favorable.

With respect to the growth curve obtained in this study, there are certain implications which merit brief consideration. If the Gompertz curve (Fig. 7) is a true representation of albacore growth, then the following points may be made: (a) the albacore is a relatively slow-growing tuna; (b) this species has a relatively long life span. Furthermore, as mentioned, it is believed that an albacore attains sexual maturity at a length of about 90 cm. If this is so, then it requires between 7 and 8 years for an albacore to become sexually mature. This is a significant portion of the life span. Since albacore enter the fisheries in substantial numbers at around 50 cm. in length (Fig. 9), a year-class is thus

exploited for about 4 years before it even attains maturity.

SUMMARY

Of 1,201 albacore tagged in the temperate North Pacific Ocean by POFI between January, 1954, and August, 1957, 15 recoveries (1.2 per cent) were reported. These recoveries indicate considerable movement of fish in the North Pacific. Albacore tagged in mid-ocean north of Hawaii have been retaken in the American West Coast fishery as well as in the Japanese fisheries. Certain recoveries were of fish which migrated across the Pacific from the American West Coast to the vicinity of Japan. There is indication that Americans and the Japanese are exploiting the same population of albacore in the temperate North Pacific Ocean.

The data on growth, although insufficient for a conclusive study, were subjected to a preliminary analysis by Walford's method of growth curve transformation, and the resulting data were also fitted in a Gompertz equation. The derived growth curves are presented.

At least those portions of the growth curves for which there are observed data appear to be a reliable representation of albacore growth. These curves are curvilinear, contrary to several linear albacore growth curves reported in the past by workers who based their studies mainly on the vertebral method. The linearity of the latter curves suggests that the age of albacore cannot be determined by the vertebral method; the rings on the centra are probably directly associated with growth rather than with age.

The results indicate that the albacore is a relatively slow-growing tuna with a rather long life span. A significant portion of the life span is passed in the immature state.

Although POFI in cooperation with the Japanese has tagged 270 albacore in the Japanese live-bait fishery, and the Japanese have recently started a tagging program in the western Pacific, none of these fish has been recovered in the American fishery. In view of the fact that the Japanese exploit generally larger albacore than the Americans, the chances for recovery in the American fishery of Japanese-tagged albacore are far less than for Japanese recovery of American-tagged fish.

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A New Species of *Acanthurus* from the Caroline Islands, with Notes on the Systematics of Other Indo-Pacific Surgeonfishes[1]

JOHN E. RANDALL

SINCE THE PUBLICATION of several articles on the systematics of surgeonfishes by the author (see References), specimens of an undescribed species of *Acanthurus* from the Caroline Islands have been obtained as well as information of value for various other acanthurids. The opportunity to acquire most of these data was provided by a fellowship from Yale University and the Bernice P. Bishop Museum for ichthyological research in French Oceania. The specimens of the new *Acanthurus* were loaned by Robert R. Rofen of the George Vanderbilt Foundation, Stanford University. For methods of counting and measuring see Randall (1956*b*: 165).

Acanthurus chronixis, n. sp.
Fig. 1

HOLOTYPE: Stanford Natural History Museum No. 52104; Teawataman Ship Pass, south side of Kapingamarangi Atoll, Caroline Islands (1° 02′ 09″ N., 154° 45′ 04″ E.), 1 mi. from shore at a depth not greater than 20 ft. over a coral, sand bottom; spear; R. Rofen and Kapingan fishermen; July 13, 1954. One female specimen, 211 mm. in standard length and 278 mm. in total length.

DESCRIPTION: Dorsal rays VIII, 26; anal rays III, 24; pectoral rays 17 (uppermost a short bony splint); pelvic rays I, 5; principal caudal rays 16; scale rows from gill opening to end of caudal spine approximately 150 (not in even rows and difficult to count); anterior gill rakers 22; posterior gill rakers 27; upper teeth 22, with 7 or 8 denticulations; lower teeth 22, with 6 or 7 denticulations.

Depth of body 2.05, head length 3.46, snout length, 4.58, length of pectoral fin 3.51, length of pelvic fin 4.69, snout to origin of dorsal fin 2.28, snout to anus 2.34, length of dorsal fin base 1.54, length of anal fin base 2.11—all in standard length. Greatest diameter of eye 4.30, width of body 2.18, width of interorbital space 3.08, postorbital length of head 5.92, least depth of caudal peduncle 2.56, length of caudal peduncle 3.06, length of caudal peduncle spine 4.06, anus to origin of anal fin 5.08, length of pelvic spine 2.04, length of first dorsal spine 4.92, length of second dorsal spine 2.76, length of third dorsal spine 2.44, length of eighth dorsal spine 1.92, length of first dorsal ray 1.75, length of first anal spine 16.5, length of second anal spine 3.18, length of third anal spine 2.30, length of first anal ray 2.00, caudal concavity 1.9, width of mouth 4.26—all in head length. Length of longest upper tooth 3.1 mm.; length of longest lower tooth 2.8 mm. Snout produced. Stomach large, round, and thick-walled.

Color in alcohol dark brown; an indistinct darker brown spot anterior and adjacent to upper end of gill opening, and a second spot, elliptical in shape and more distinct, posterior to upper end of gill opening; opercular membrane darker brown than rest of body; a very dark brown band at extreme base of dorsal fin. Life colors unknown.

POSSIBLE JUVENILES: Two small surgeonfish, one juvenile, 46.9 mm. in standard length and 61.2 mm. in total length, and one postacronurus, 34.5 mm. in standard length and 45.4 mm. in total length, were collected from the reef flat west of the northern end of Falarik Islet, Ifaluk Atoll, Caroline Islands (7° 15′ 33″ N., 144° 26′ 10″ E.), about .4 mi. from shore at a depth of 6 ft. over a bottom of coral, encrusting algae, and sand with the use of rotenone by Ifaluk fishermen for R. Rofen on October 30, 1953. Figure 2 is a photograph of the two specimens. The juvenile has a produced snout, and both specimens possess eight dorsal spines. Only three known species of *Acanthurus* have eight dorsal

[1] Contribution No. 268 from The Marine Laboratory, University of Miami. Manuscript received October 30, 1958.

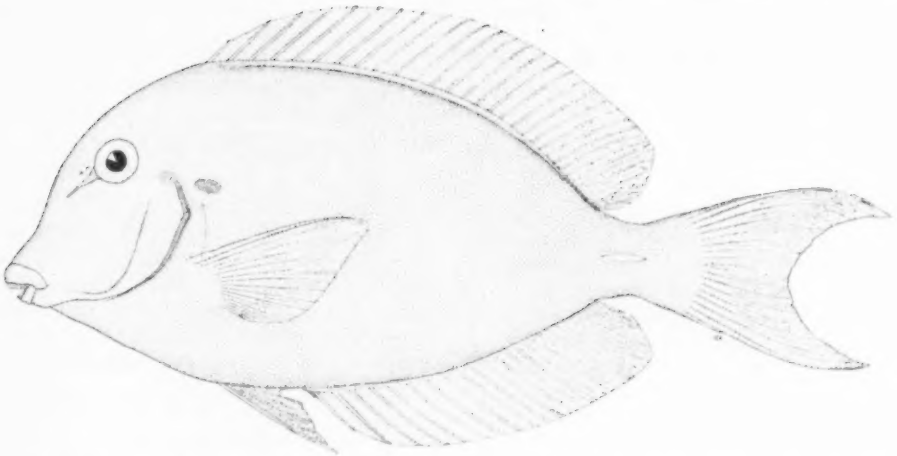

FIG. 1. Holotype of *Acanthurus chronixis* from Kapingamarangi, Caroline Islands; standard length 211 mm.

spines, *A. sohal* (Forskål), *A. pyroferus* Kittlitz, and *A. chronixis*. The young of *sohal* is known (Randall, 1956*b*: fig. 1), and the young of *pyroferus* is described later in this paper. Although a series of specimens is lacking to link the two small ones from Ifaluk to the holotype, it seems likely that they represent the young of *A. chronixis*. There are meristic differences, however, that arouse some suspicion. The two small specimens have 15 pectoral rays and 27 or 28 soft dorsal rays, as opposed to 17 pectoral rays and 26 soft dorsal rays for the holotype. The possibility that these two specimens are the young of a species as yet undescribed cannot be discounted. For this reason they are not designated as paratypes of *chronixis*. They are deposited in the Stanford Natural History Museum (SNHM) under the number 52105. Their description follows (data for the transforming specimen in parentheses).

Dorsal rays VIII, 27 (28); anal rays III, 25 (25); pectoral rays, 15 (15); upper teeth, 12 (16, the two medial ones large and like adult teeth); lower teeth, 12 (18, a single large medial one).

Depth of body 1.78 (1.64), head length 3.21 (2.98), snout length 4.74 (5.95), length of pectoral fin 2.59 (2.63), length of pelvic fin 3.72 (4.10), snout to origin of dorsal fin 2.06 (2.33), snout to anus 2.18 (2.01), length of dorsal fin base 1.40 (1.41), length of anal fin base 1.95 (1.89)—all in standard length. Greatest diameter of eye 2.44 (2.70), width of body 2.00 (2.19), width of interorbital space 2.86 (3.14), postorbital length of head 3.74 (4.46), least depth of caudal peduncle 2.70 (2.76), length of caudal peduncle 4.30 (4.92), length of caudal peduncle spine 6.95 (7.26), length of pelvic spine 1.85 (2.70), length of first dorsal spine 5.40 (4.83), length of second dorsal spine 2.61 (2.32), length of third dorsal spine 1.87 (2.15), length of eighth dorsal spine 1.23 (1.84), length of first dorsal ray 1.20 (1.76), length of first anal spine 5.21 (5.80), length of second anal spine 2.66 (2.83), length of third anal spine 1.72 (2.07), length of first anal ray 1.46 (1.90), width of mouth 3.56 (3.87)—all in head length. Caudal fin markedly rounded.

Color in alcohol of juvenile light brown with numerous faint pale spots on body, some confluent dorsally to form short vertical or diagonal pale bars; median fins with dusky membranes, the dorsal and anal with rows of pale spots and the caudal with a narrow pale margin and a faint spotting in middle portion of fin; edge of upper portion of opercle dusky. Color of postacronurus uniform light tan with a ver-

tical dusky band at base of caudal fin. Life colors unknown.

DISCUSSION: The transformation of the acronurus larval form into the juvenile stage involves some striking morphological changes. Notable are the formation of scales from narrow vertical ridges on the body and a prolongation of the snout. The difference in relative length of the snout of the two small specimens should be kept in mind when comparing proportional measurements involving head length.

A. chronixis is closely related to *A. pyroferus*, having a similar configuration, especially with respect to the produced snout, similar meristic data, and the same stomach structure. The young of both species appear to be the only ones of the genus with rounded caudal fins, and both develop strongly lunate fins as adults. *A. chronixis* differs from *pyroferus* principally in coloration; it lacks the broad pale terminal band of the caudal fin, the white line nearly encircling the mouth, and the large pale area on the pectoral fin. Also there are different markings on the shoulder region of the two species. The type locality of both species is the Caroline Islands.

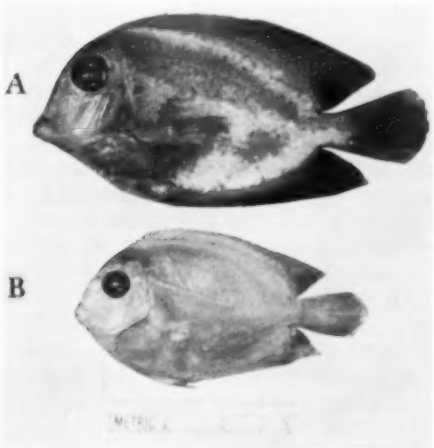

FIG. 2. *A*, Juvenile of *Acanthurus chronixis;* standard length 46.9 mm. *B*, Postacronurus of *A. chronixis;* standard length 34.5 mm. Both specimens from Ifaluk, Caroline Islands. Photo by W. Courtenay.

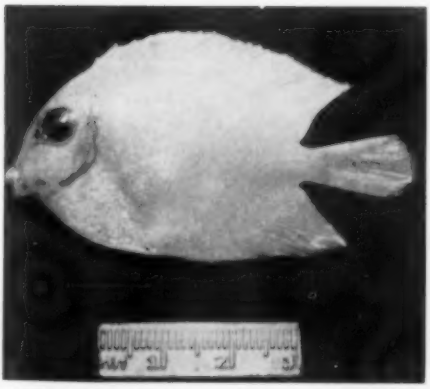

FIG. 3. Juvenile of *Acanthurus pyroferus* Kittlitz from the Society Islands; standard length 43 mm. Reproduced from a 35 mm. Kodachrome transparency. Color in life bright yellow with blue markings on head.

NOTES ON OTHER SPECIES

Randall (1956*b*: 197) cast some doubt on the statement of Kittlitz (1834) that the young of *Acanthurus pyroferus* are dirty yellow in color, by suggesting that this author might have confused the young of this species with *A. olivaceus* Bloch and Schneider. Recent collections of *A. pyroferus* in the Society Islands (Fig. 3 represents the smallest specimen taken) have revealed that Kittlitz was largely correct. The young are yellow in color, although bright yellow. Kittlitz, of course, may have seen specimen(s) transforming from juvenile to the dark brown adult coloration, at which time the principal color might be described as dirty yellow. The change-over in color in three specimens occurred at standard lengths of 88, 94, and 95 mm. One from the Marquesas had nearly attained adult color patterns at a standard length of 98 mm.

In addition to the bright yellow color, juveniles of *A. pyroferus* have a brilliant blue ring around the eye, a blue margin on the opercle, a blue ring nearly encircling the mouth, a small bright orange area just above the base of pectoral fin, and a narrow pale margin and thin, black submarginal line posteriorly on the median fins. This striking color pattern is precisely the same as that of the small angelfish *Centropyge flavis-*

simus (Cuvier and Valenciennes), thus suggesting the phenomenon of mimicry. Also both *C. flavissimus* and the young *of A. pyroferus* have rounded caudal fins. If mimicry is involved, then the surgeonfish would seem to be the mimic and the angelfish the model, for the former is less common, and it loses the color and caudal-fin shape of *C. flavissimus* when it grows to a size greater than attained by the angelfish. Attempts to deduce the basis for the alleged mimicry were not successful. The problem will be discussed in greater detail in a forthcoming paper on mimicry.

Adults of *A. pyroferus* have very lunate caudal fins. The transformation in shape of the caudal fin of this species begins before adult color pattern is assumed. A 70 mm. specimen, still bright yellow, has a caudal fin less rounded than smaller specimens. The lobes of the caudal fin of a 92 mm. yellow specimen and a 95 mm. brownish-yellow specimen are just starting to form.

The counts of the soft rays of the dorsal and anal fins of *A. pyroferus* from the Society Islands are higher than the counts from specimens in the Marshall Islands and Philippines (Table 1), indicating that the population in the former island group may be distinct from the latter two, which in turn, appear differentiated. A more detailed analysis must await the collection of additional specimens from these and intermediate island areas of the tropical Pacific.

Specimens of *A. pyroferus* from the Society Islands have been sent to the U. S. National Museum (USNM) and the SNHM.

The possible hybrid surgeonfish *Acanthurus achilles* × *Acanthurus glaucopareius* (Randall, 1956*a*: 21–25) is known from three specimens, originally described as *A. rackliffei* by Schultz (1943: 157, 163, fig. 13) from Hull Atoll, Phoenix Islands, in the central Pacific. The hypothesis that these specimens are hybrids would be strengthened if specimens were obtained in other areas where both *A. achilles* Shaw and *A. glaucopareius* Cuvier are known to occur.

TABLE 1
FIN-RAY COUNTS OF SPECIMENS OF *Acanthurus pyroferus* FROM THE PACIFIC OCEAN

LOCALITY	DORSAL SOFT RAYS				ANAL SOFT RAYS				
	27	*28*	*29*	*30*	*24*	*25*	*26*	*27*	*28*
Society Is.		4	8	5		2	8	6	1
Marshall Is.	2	2				2	2		
Philippine Is.	5				1	4			

In February, 1956, at Caroline Atoll (10° S., 150° 14′ W.), a single adult of the postulated hybrid was sighted in the clear water off the lee reef. It was wounded with a spear but not captured. It was intermediate in life color to the parent species (no information on life color was available for the original three specimens of *rackliffei*). In subsequent months, three specimens were speared in the Tuamotu Archipelago. One, 110 mm., was obtained from Makatea directly off the phosphate loading area. It was the only hybrid seen at this island. Three were observed at the atoll of Takaroa; one of these, a 140 mm. specimen, was taken in the lagoon near the pass. The third specimen, 132 mm. in standard length, was collected from the outer reef at Takapoto. A single hybrid was seen in the pass at Tikahau but was not taken. At all of the islands where the hybrids were sighted, *A. achilles* and *A. glaucopareius* were very abundant, hundreds of both species being seen in each area.

One of the Takaroa hybrids was consistently seen at the entrance to the pass. It was a large adult with a scar on the back, thus permitting positive identification during the week that it was observed. This fish was constantly harassed by individuals of *A. glaucopareius*, the latter being perhaps the most pugnacious species of the genus. At times the hybrid experienced almost no respite, for it would flee from one aggressor only to meet with another nearby.

The dorsal and anal fin-ray counts of the new specimens (Makatea and Takapoto, D IX, 30; A III, 27; Takaroa D IX, 29; A III, 27) and their color and morphology are the same as that of the Hull Island hybrids. The life colors of the Takaroa specimen are as follows: body purplish black; a small orangish-yellow region surrounding and extending anterior to spine on caudal peduncle (reaches 7 mm. in front of spine and is a maximum of 4 mm. in height); a very faint pale area under eye; a purplish-white ring encircling lower half of mouth;

dorsal and anal fins colored like body except for narrow, pale blue margins and an orangish-yellow area at the base of these fins which is broader posteriorly; caudal fin colored like body basally, pale distally, these two regions separated by a broad area which appears salmon underwater, and is the best recognition mark of the hybrid (examined closely this colored area is reddish orange outwardly and orangish yellow inwardly, with lobes of orange extending into the yellow).

The Makatea and Takapoto specimens have been deposited in the SNHM (48869), and the Takaroa hybrid at the USNM (169883) (two of the original hybrids are located at the USNM and the third at the Museum of Comparative Zoology at Harvard).

Two specimens of *Acanthurus nubilus* (Fowler and Bean), previously known only from Celebes in the East Indies, were collected by spearing in Moorea, Society Islands, outside the barrier reef. This species seemed moderately common in this area at depths of about 70–130 ft. Like *A. thompsoni* (Fowler), with which it was occasionally associated, it was frequently observed well off the bottom.

When seen underwater, *nubilus* was predominantly light blue except for a white caudal fin and a region of yellow around the caudal spine. After spearing and removing the fish from the water, it was noted that the white tail had altered to dark gray, and the body was dark yellowish brown with numerous lengthwise blue lines (60 counted vertically from origin of anal fin on 158 mm. specimen, and 66 on 169 mm. specimen). The blue lines were about half the width of intermediate brown bands. The head and thorax were bright blue with numerous, close-set, round, dark yellowish-brown spots (in diameter about one-third the diameter of pupil of eye). A broad, brownish-yellow area was visible around the caudal spine; the socket of the caudal spine was whitish; the sheath whitish medially, shading through yellow to black at edge. The dorsal and anal fins were bluish gray basally and greenish brown distally with numerous dark brown bands. The pectorals were hyaline with blackish rays and the pelvics pale blue with blackish rays.

The following counts and proportional measurements were made on the specimens: D VII, 27; A III, 23 and 24; P 16; anterior and posterior gill rakers 23 (one specimen only); caudal concavity 6.7, head length 4.5, depth 2 to 2.1—all in standard length; longest dorsal ray equal to head length; eye 3 in head length.

These two fish differ from the 153 mm. holotype in the USNM in less body depth (1.8 in holotype) and shorter head (head length of holotype 4.1). In view of the great similarity in other features such as color pattern, I regard the above differences in measurement as probably within the range of variability of the species. The specimens have been deposited in the SNHM.

The acanthurids from collections of fishes made at islands in the Indian Ocean in 1957 by James E. Morrow and associates were loaned to the author from the Bingham Oceanographic Laboratory, Yale University. The following species were collected in the Maldives: *Acanthurus triostegus* (Linnaeus), *A. lineatus* (Linnaeus), *A. gahhm* (Forskål), *A. leucosternon* Bennett, *A. nigrofuscus* (Forskål), *Ctenochaetus striatus* (Quoy and Gaimard), and *Zebrasoma veliferum* (Bloch). From the Seychelles the following were taken: *Acanthurus triostegus, A. lineatus, A. leucosternon, A. nigrofuscus,* and *A. tennenti* Günther. The collections were made with rotenone from inshore waters.

Acanthurus leucosternon is as well represented in the collections as other surgeonfishes, which stands in opposition to the statement of Randall (1956*b*: 196) that the species does not appear to be common, a view based on the paucity of specimens in the United States. The new specimens are most welcome in providing material for additional fin ray counts (Table 2).

A. leucosternon appears to be confined to the Indian Ocean and East Indies. The closely related *A. achilles* remains unrecorded from the Indian

TABLE 2
FIN-RAY COUNTS OF SPECIMENS OF *Acanthurus leucosternon* FROM THE INDIAN OCEAN

LOCALITY	DORSAL SOFT RAYS				ANAL SOFT RAYS		
	28	*29*	*30*	*31*	*26*	*27*	*28*
Maldive Is.	1		1		1	1	
Seychelle Is.		3	7	1	1	7	3

FIG. 4. Juvenile of *Acanthurus leucosternon* Bennett from the Maldive Islands; standard length 54 mm. Dark area around pectoral fin is shadow. Photo by W. Courtenay.

Ocean, and *A. glaucopareius*, also a near relative, is known in the Indian Ocean only from Cocos–Keeling and Christmas islands.

The juvenile stage of *A. leucosternon* (Fig. 4) is very similar to the adult. The acronurus, unless it is the *Acronurus formosus* of Castelnau (Randall 1956*b*: 202), has not been described. It may be large like the acronuri of *A. achilles* and *A. glaucopareius*.

Marden (1956: 185) has portrayed *Acanthurus leucosternon* in an underwater color photograph. The body of the fish is bright blue. A broad blackish band curves down from the interorbital region, enclosing eye, and covering most of the operculum. The dorsal fin is bright yellow edged with blue, and the caudal peduncle and region of caudal spine are also yellow. The caudal fin is black with a large crescent of white and a blue margin posteriorly. The anal and pelvic fins are white, and there is a white area on the chest and a white band on the chin.

Dorsal and anal fin-ray counts of *A. lineatus* from the Indian Ocean and the Pacific (Table 3) suggest differentiation of the species in these two oceans. *A. lineatus* is known from the coast of East Africa, but not from the Red Sea where a similar but very distinctive species, *A. sohal*, appears to be endemic.

The dorsal soft rays of three specimens of *Zebrasoma veliferum* from the Maldives number 27–30, and the anal soft rays 22–24. These counts align themselves with those from other Indian Ocean localities which differ significantly from counts of specimens from the Pacific (Randall 1955*c*: table 1).

Dorsal soft rays of 10 specimens of *Acanthurus tennenti* collected by Morrow in the Seychelles number 22–24 (mostly 23), and the anal soft rays 21–23 (mostly 22).

Smith (1955: 692) listed the acanthurids from the island of Aldabra in the Indian Ocean north of Madagascar and described two of them as new. One, *Acanthurus bicommatus* (pl. XVIII, C and D in Smith), is a synonym of *A. tennenti*. The second, *A. melanosternon* (pl. XVIII, B), is a valid species, differing from others principally in the nearly black color of the chest which encloses a broad white patch below the middle of the lower preopercular margin, this patch in some specimens continuing as a band midventrally, thus dividing the black area anteroposteriorly. This white band on the chest is suggestive of *A. leucocheilus* Herre from the Philippines, as is the outer pale one-third of an otherwise dark pectoral fin. *A. melanosternon* lacks the bluish-white band at the base of the caudal fin, the black snout with a white band encircling the mouth, and the dark red lines distally in the dorsal and anal fins of *leucocheilus*. Meristic data were given by Smith as follows: D IX, 25–26; A III, 24–25; P 17; gill rakers 21–22. He had numerous specimens, 280–480 mm. in length, taken over a wide area of East African coast as far south as 15° and at various islands in the Indian Ocean.

Also listed by Smith among the species of *Acanthurus* from Aldabra and East Africa is *A. philippinus* Herre (= *A. thompsoni* (Fowler)). This represents the first record of *A. thompsoni* from the Indian Ocean.

Three species of *Ctenochaetus* were recorded

TABLE 3
FIN-RAY COUNTS OF SPECIMENS OF *Acanthurus lineatus* FROM INDO-PACIFIC LOCALITIES

LOCALITY	DORSAL SOFT RAYS						ANAL SOFT RAYS			
	25	*26*	*27*	*28*	*29*	*30*	*25*	*26*	*27*	*28*
Maldive Is.	1	1	8	2			1	5	5	1
Seychelle Is.			2	2				1	2	1
Mauritius			1					1		
Palau Is.			1	4	2				6	1
Mariana Is.			5	9	3			1	10	6
Samoa Is.			5	2	1			2	5	1
Society Is.			4	4				3	5	
Marquesas Is.						1				1

by Smith from Aldabra: *C. striatus*, *C. strigosus* (Bennett), and *Ctenochaetus* sp. (the latter species was left undesignated pending the publication of the revision of the genus). He provided information on the latter species in a letter enabling me to identify it as *C. cyanoguttatus* Randall. His specimen is 9 in. in length and was described as having "light blue spots all over in life." This is the first record of *cyanoguttatus* west of the Gilbert Islands, although the blue-spotted *Acanthurus ctenodon* Var.*b* of Playfair (1866: 57) from Zanzibar is probably also *C. cyanoguttatus*.

After the revision of *Ctenochaetus* was published (Randall, 1955*d*), a large specimen of *C. cyanoguttatus* from Cocos Island was found at the USNM—probably one of the four specimens of Snodgrass and Heller (1904) originally cataloged at the SNHM. As mentioned in the revision (p. 161), no trace of blue spots could be found on the one Cocos Island specimen seen at Stanford. The National Museum specimen, however, possesses pale bluish spots on the side beneath the pectoral fins which are closely applied to the body. The cover provided by these fins probably prevented the fading of the spots at this location.

Three specimens of *C. cyanoguttatus*, 212, 202, and 120 mm. in standard length, were collected by spearing at Ua Pou in the Marquesas Islands. Numerous small, bright blue spots covered the head, body, and pectoral fins, those posteriorly on the body being smaller. A pale blue band was evident at the base of the dorsal and anal fins. These fins were banded alternately with pale blue and dark yellowish brown. The iris was dark blue. Many individuals underwater displayed whitish lips and a whitish caudal fin. The caudal may also be brown with lengthwise blue streaks. This species was not seen in the Society Islands or Tuamotus but proved to be abundant at the three islands visited in the Marquesas, Ua Pou, Nuku Hiva, and Eiao. On the two occasions when *C. cyanoguttatus* was observed in the Gilbert Islands, it occurred in schools. It was not observed to school in the Marquesas.

C. striatus, probably the most abundant reef fish of its size in the Society Islands, was never seen in the Marquesas, although much effort was expended to locate it there. The specimen reported by Fowler (1938: 76) as *C. strigosus* from Ua Pou and said to have blue lines on the body was examined at the Academy of Natural Sciences of Philadelphia. It is *C. cyanoguttatus*, and blue spots, not lines, are still evident on the body.

When the two larger specimens of *C. cyanoguttatus* were collected by the author, difficulty was experienced in deciding whether they should be labelled as *C. cyanoguttatus* or *C. magnus* Randall. They were more like *magnus* in general appearance, with greater depth, convex profile, and scales in very irregular rows. There were, however, predominantly four denticulations on the expanded tips of the upper teeth as is seen on teeth of *cyanoguttatus* and not three, a number which was presumed to be diagnostic for *magnus*. Also the bands in the dorsal and anal fins persisted in preservative (these are not visible on the preserved specimens of *magnus*). Leonard P. Schultz kindly loaned the types of *cyanoguttatus* (170.5 mm.) and *magnus* (225 mm.) from the USNM in order that they might be compared with the two large and one small Marquesan specimens. It was noted that some of the upper teeth of the holotype of *magnus* bear four instead of three denticulations. It now seems that the differences between these two forms are principally ones of age, and *magnus* should be referred to the synonymy of *cyanoguttatus*.

Meristic data of the three Marquesan specimens of *cyanoguttatus* are given in Table 4.

Randall (1955*b*: 189) collected a 35 mm. specimen of *Ctenochaetus* from the Gilbert Islands which was not identified to species. It was brown with a bright yellow caudal peduncle and caudal fin. The specimen is shown in Figure

TABLE 4
COUNTS FROM SPECIMENS OF *Ctenochaetus cyanoguttatus* FROM THE MARQUESAS ISLANDS

STANDARD LENGTH (mm.)	NUMBER OF TEETH		NUMBER OF SOFT RAYS	
	Upper	Lower	Dorsal	Anal
120	41	54	27	24
202	46	65	26	24
212	42	67	27	24

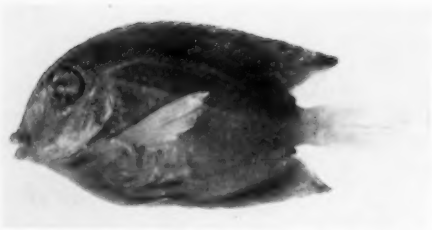

FIG. 5. Juvenile of *Ctenochaetus binotatus* Randall from the Gilbert Islands; standard length 35 mm.

5 of the present paper. As a result of the examination of specimens of *C. binotatus* taken in the Society Islands, it is now apparent that the one from the Gilbert Islands is a juvenile of this species. The upper teeth with seven instead of six denticulations and the bright yellow caudal coloration are juvenile characteristics.

No positive record of the life color of adults was available for the description of *C. binotatus*. The following color notes made from specimens speared in Papetoai Bay, Moorea, are therefore presented. A 130 mm. adult was chestnut brown on the head and body with narrow, blue, lengthwise lines on the body and small blue spots on the head and thorax; the median fins were brown; the caudal, however, was observed to be dull yellow underwater and after the fish was speared the color of the fin alternated from entirely brown to brownish yellow on the upper half and brown on the lower; also evident while the fish was still alive was a temporary suffusion of brownish yellow over the body and dorsal and anal fins; faint diagonal-lengthwise bands of dull orange were visible in the dorsal fin, and the dorsal and anal had a narrow blue-black margin and the diagnostic black spot at rear base of each of these fins; the pectoral membranes were hyaline, the rays yellowish brown; the iris was deep blue. A 31 mm. specimen in a late phase of transformation from the acronurus to the juvenile state was brown with vivid yellow caudal fin, caudal peduncle, and posterior part of dorsal and anal fins (thus emphasizing the black spot at rear base of the latter two fins); blue spots were present anteriorly on the body and blue lengthwise lines posteriorly.

Juveniles are commonly seen on the shore reef of Papetoai Bay at a depth of about 3–6 ft.; adults occur in the bay at a depth of 30–40 ft. at the base of the vertical front of the shore reef. *Acanthurus thompsoni* was observed and collected from the same general habitat, though more over the sand adjacent to the vertical reef front.

Ctenochaetus strigosus is here recorded from the Society Islands and Marquesas for the first time. This species in French Oceania also displays a striking color change from juvenile to adult. The young are entirely bright yellow—the fourth species of surgeonfish known to have a yellow juvenile stage (the others are *Acanthurus pyroferus*, *A. olivaceus*, and *A. coeruleus* Bloch and Schneider; curiously, none of these species appear to be closely related). In the Hawaiian Islands, however, the young of *C. strigosus* are not yellow but are brown like adults. As previously discussed (Randall, 1955*d*: 159) a notable color difference exists between adults in the Hawaiian Islands and the Philippines and those in the Tuamotus. The caudal fin of Hawaiian and Philippine fish is brown, whereas it is white in specimens from the Tuamotus (and the Societies and Marquesas). Specimens from all of these areas (except the Philippines), when alive have a bright yellow ring around the eye or a rim of yellow adjacent to the posterior edge of the eye. Even the yellow juveniles clearly show a posterior rim of yellow, for the yellow color is brighter adjacent to the eye than on the rest of the head.

In the Society Islands the change from yellow juvenile to dark brown, white-tailed adult coloration takes place at a standard length of about 50 mm. There is considerable variation in size at which this occurs, however. Yellow specimens have been taken which are as large as 54 mm., and brown with white tail have been taken as small as 45 mm. in standard length. At Takaroa, Tuamotus, a specimen was collected which was changing from yellow juvenile to brown adult color at a standard length of 67 mm. A 32 mm. specimen was speared in Moorea at a depth of 20 ft. which was in a late stage of transformation from the acronurus to the juvenile form (there was still a trace of silver over the abdomen, and the scales on the body were not fully formed). The specimen was dull yellow-orange with bright orange caudal fin, a

TABLE 5
FIN-RAY COUNTS OF SPECIMENS OF *Ctenochaetus strigosus* FROM THE PACIFIC OCEAN

LOCALITY	DORSAL SOFT RAYS				ANAL SOFT RAYS				
	25	*26*	*27*	*28*	*21*	*22*	*23*	*24*	*25*
Hawaiian Is.	4	19	23	1			9	32	6
Philippines and East Indies	3	6	4				7	6	
Tuamotu Arch.	4	5	4		1	1	5	5	1
Society Is.		4	4				1	5	2
Marquesas Is.		1						1	

blue eye, a narrow yellow rim on posterior half of eye, and a narrow black margin on dorsal and anal fins.

Dorsal and anal fin-ray counts (Table 5) of *C. strigosus* are not as indicative of population differentiation as color characters and shape of the caudal fin (Randall, 1955*d*: 159).

Ctenochaetus hawaiiensis Randall (1955*d*: 155, 161, fig. 2), formerly known only from the island of Hawaii, was collected by the author in the Tuamotu Archipelago and Society Islands. A 153 mm. specimen was speared at a depth of 120 ft. just north of the entrance to the pass at the atoll of Tikahau, a 194 mm. specimen at a depth of 15 ft. at the edge of a patch reef in the lagoon of Takaroa, and a 163 mm. specimen at a depth of 125 ft. outside the barrier reef at Moorea. In the Tuamotus and Societies this species was occasionally encountered at depths of about 100–130 ft. The only individual seen in these islands in shallow water was the Takaroa specimen. The three specimens collected from French Oceania differed in life color from the species in Hawaii only in their possession of dark blue on the membranes of the pectoral fins. This color was most pronounced in the upper part of the fins. In body proportions and all meristic data they agree with Hawaiian material.

Specimens of *C. binotatus*, *C. strigosus*, and *C. hawaiiensis* from French Oceania have been deposited in the USNM and the SNHM.

Also taken at Takaroa was a perplexing 175 mm. specimen of *Acanthurus* which is very similar to *A. olivaceus*. Instead of a long band of orange surrounded with deep blue on the shoulder area, the orange in this specimen was restricted to a small elongate patch extending posteriorly from the upper end of the gill opening for a distance equal to one eye diameter (Fig. 6); the dark blue band, the diameter of an eye in width, extended as a solid area as far as the tip of the pectoral fin (when this fin was applied to the body). When the specimen was first seen, the caudal fin was cream except for dark edges and a semicircular black area in the median posterior part of the fin. After being speared, the pale portion of the fin darkened to light yellowish brown. The caudal fin of *A. olivaceus* is normally dark brown with a semicircular area of white (except for narrow black posterior margin) in the same location as the black area of the specimen in question. In other respects the color was like *olivaceus*. There was a deep brownish-red band at the extreme base of the dorsal and anal fins; the anal was narrowly edged with blue; the outer third of the pectoral fins was hyaline with a tinge of yellow. The specimen was observed swimming with several *A. olivaceus* before it was speared. Later four specimens of *olivaceus* were speared in the same area to provide comparison. No differences other than color could be ascertained. The fin-ray and gill-raker counts of the specimen (D IX, 24; A III, 23, P 17; gill rakers 26) are within the range of the four

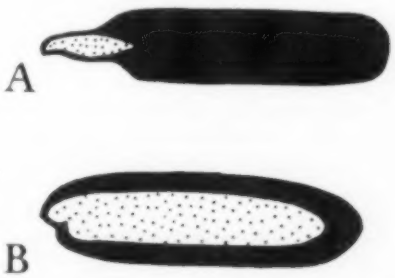

FIG. 6. *A*. Color mark which extends posteriorly from upper end of gill opening of a 178 mm. variant of *Acanthurus olivaceus* Bloch and Schneider, taken at Takaroa, Tuamotus. The same mark occurred on all of the *A. olivaceus* specimens seen in the Marquesas. *B*. Usual color mark on shoulder of *A. olivaceus*. The stippled region represents bright orange, the black area dark blue.

olivaceus (D IX, 24–25; A III, 23–24; P 17; gill rakers 25–28). Two of the four *olivaceus* displayed a restriction in width and intensity of color of the posterior part of the orange shoulder band. None, however, showed a darkening of the white posterior area of the otherwise dark caudal fin.

At the time it was collected, the specimen was regarded as an aberrant color form of *olivaceus*. Later at Ua Pou and Nuku Hiva in the Marquesas, all of the *olivaceus* which were seen were colored like this one Takaroa specimen. Therefore it now seems likely that *A. olivaceus* is subspecifically different in the Marquesas and that occasional individuals drift as larvae to the northern Tuamotus where they may intergrade with the common *olivaceus* form there. Because of a limited supply of formalin, only a single specimen was brought back from the Marquesas. It was speared in Anaho Bay, Nuku Hiva, on July 16, 1957. It is 196 mm. in standard length. The shoulder mark is 60 mm. in length, and the orange part of it 17 mm. The caudal fin was pale yellowish with a black crescent mid-posteriorly.

The Takaroa specimen was deposited in the USNM and the Nuku Hiva one at the SNHM. No nomenclatorial designation of the Marquesan subspecies is offered at this time. Additional specimens should be procured from both the Marquesas and Tuamotus.

A specimen of *Acanthurus olivaceus* in the intermediate stage between yellow juvenile and brown adult coloration was collected in the pass of Takaroa. It is 134 mm. in standard length.

A year's collecting of fishes in the Society Islands and Tuamotus, resulting in the taking of over 350 species of reef fishes, failed to yield any specimens of the yellow *Zebrasoma flavescens* (Bennett), although the brown *Z. scopas* (Cuvier) proved to be common (additional fin-ray counts of the latter continue to be predominantly D IV, 24; A III, 20). When a relatively large individual of the species *Acanthurus pyroferus* still in the yellow color phase was first sighted underwater in Tahiti by the author, it was mistaken for *Z. flavescens*. The error was not perceived until the specimen was speared and regarded closely. *Z. flavescens* is recorded to date from the Hawaiian Islands, Johnston Island, Wake Island, northern Marshall Islands, and Mariana Islands. Eibl-Eibesfeldt (1955: 217), in a paper concerning fish behavior, mentioned yellow *Z. flavescens* from Cocos Island off Costa Rica. This record was based on underwater observation and should be substantiated with the collection of specimens.

A specimen of *Zebrasoma scopas*, 25 mm. in standard length, which was transforming from the late postlarval or acronurus stage to the juvenile form, was collected in Papetoai Bay, Moorea, at a depth of 30 ft. on September 18, 1956. It was dark brown, shading to purplish brown anteriorly, with vertical pale lines; the chest was silvery and mottled with brown; the ends of the median fins were narrowly hyaline. Another, 26 mm. in standard length, was taken in the bay March 21, 1957.

Zebrasoma rostratum (Günther) has been recorded previously only from the Society Islands and the Tuamotus. This distinctive long-snouted surgeonfish was collected by the author at Takaroa and Takapoto in the Tuamotus, where it is common on the outer reef. In spite of extensive collecting in the Society Islands, the type locality, it was not taken, nor was it observed. The range of the species is here extended to include the Marquesas (one specimen taken at Anaho Bay, Nuku Hiva), Caroline Atoll (one specimen taken off the lee reef), and Palmyra, Line Islands (two specimens collected by R. R. Rofen).

A large adult *Naso rigoletto* Smith (1951: 1126-1132, fig. 1), the most characteristic feature of which is a marked depression in the contour of the back at the base of the spinous portion of the dorsal fin followed by a hump, was sighted by the author in the lagoon of Moorea, Society Islands, at a depth of 90 ft., but the fish was not taken. Subsequently two large specimens were purchased from the market in Papeete, Tahiti. One was shipped to the SNHM, and the other (Fig. 7) to the USNM. This is the first record of the species from the Pacific. It was previously known only from East Africa. The National Museum specimen is a 565 mm. female lacking a horn on the fore-

FIG. 7. *Naso rigoletto* Smith from Tahiti; standard length 565 mm. Reproduced from a 35 mm. Kodachrome transparency.

head (according to Smith, only the males of this species possess a long rostral prominence). This fish was gray on the dorsal half of the body and light gray ventrally. There were about five small blue spots anteriorly on the body above the pectoral fin and two such spots posteriorly on the head. The caudal spines were not colored. Fin-ray counts are as follows: D V, 30; A II, 29; P 17.

N. rigoletto was sighted underwater at Eiao, Marquesas, as was *N. lituratus* (Bloch and Schneider), but was not taken.

The surgeonfishes previously known from the Marquesas Islands include *Ctenochaetus cyanoguttatus, Acanthurus lineatus, A. triostegus,* and *A. glaucopareius;* all of these are common. The acanthurids which represent new additions to the Marquesan fauna are *A. pyroferus, A. olivaceus, Ctenochaetus strigosus, Zebrasoma rostratum, A. achilles, A. guttatus* Bloch and Schneider, *A. nigroris* Cuvier and Valenciennes, *A. xanthopterus* Cuvier and Valenciennes (a 474 mm. specimen; only the head preserved), *A. bleekeri* Günther, and *Naso unicornis* (Forskål). The specimen of *Acanthurus bleekeri* is 280 mm. in standard length. It was one of a school of about 30 fish at Eiao which varied in hue from pale bluish to dark brown. The broad yellow band through the eye was conspicuous regardless of ground color.

The specimen of *Naso unicornis* measured 448 mm. in standard length; it possessed a horn which extended directly forward from the eye. The lower edge of the horn measured 52 mm. from the head. Counts of the specimen were as follows: D VI, 30; A III, 29; P 18. The color in life was gray on the back shading to yellow ventrally, with a patch of blue blotches in the region of the pectoral fin; the dorsal and anal fins were alternately striped with diagonal bands of orange and blue; the caudal fin was gray, becoming yellowish outwardly. Only the caudal region and snout were preserved.

Most of the acanthurids from the Marquesas Islands have been deposited in the SNHM.

Although only 12 days were spent in collecting and observing fishes in the Marquesas, it seems likely that certain surgeonfishes such as *Ctenochaetus striatus, Acanthurus nigrofuscus,* and *A. gahhm,* common throughout the South Seas, are absent in this island group. Little observation is needed to notice that the Marquesas have an impoverished fish fauna. This is more evident for many other families of fishes, such as the Labridae and the Chaetodontidae, than it is for the acanthurids. The explanation for the scant fauna probably lies both in the eastern position of the Marquesas in the Indo-Pacific in a region of westward-moving current and in the paucity of coral reefs.

SUMMARY

1. *Acanthurus chronixis* is described as new from Kapingamarangi Atoll, Caroline Islands. The description is based on a single 211 mm. specimen. Two juveniles from Ifaluk in the Carolines, probably belonging to this species, are described in detail. Due to slight meristic differences from the holotype, these small specimens are not designated as paratypes.

A. chronixis is one of three known species of *Acanthurus* with eight dorsal spines. It appears to be closely related to *A. pyroferus,* sharing with it the dorsal-spine count, a somewhat produced snout, and a spherical, thick-walled stomach. It differs from *A. pyroferus* primarily in color pattern.

2. The juvenile stage of *Acanthurus pyroferus* is bright yellow in life with blue and orange markings and a rounded caudal fin. It closely resembles the angelfish *Centropyge flavissimus,* thus suggesting mimicry.

3. The population of *Acanthurus pyroferus* in the Society Islands appears differentiated from populations in the Marshall Islands and Philippines on the basis of a higher number of soft rays in the dorsal and anal fins.

4. Three specimens of the hybrid surgeonfish *Acanthurus achilles* × *Acanthurus glaucopareius*, previously known only from Hull Island in the Phoenix group, were collected in the Tuamotu Archipelago. The life color of the hybrids was noted to be intermediate to the parent species.

5. *Acanthurus nubilus*, heretofore known only from Celebes, was collected in Moorea, Society Islands, where it is not uncommon outside the barrier reef at depths of about 100 ft. The life colors are given.

6. The acanthurids from a collection of fishes in the Indian Ocean by J. Morrow are reported on briefly. Fin-ray counts are given for *Acanthurus leucosternon*, *A. lineatus*, *A. tennenti*, and *Zebrasoma veliferum*.

7. *Acanthurus bicommatus* Smith (1955: 694) is a synonym of *A. tennenti*. *A. melanosternon* Smith (1955: 693) from East Africa and islands in the Indian Ocean is a valid species.

8. *Ctenochaetus* sp. Smith (1955: 693) from Aldabra, Indian Ocean appears to be *C. cyanoguttatus*.

9. *Ctenochaetus magnus* Randall (1955*d*: 155, 162) is referred to the synonymy of *C. cyanoguttatus*.

10. The specimen from Ua Pou, Marquesas, reported by Fowler (1938) as *Ctenochaetus strigosus* is *C. cyanoguttatus*. This species is common in the Marquesas, but *C. striatus*, usually abundant in the tropical Pacific, was not observed in this island group.

11. The 35 mm. *Ctenochaetus* sp. Randall (1955*b*: 189; 1955*d*: 164) from the Gilbert Islands is a juvenile *C. binotatus*. This species is recorded from the Society Islands, and the juvenile and adult life colors are given.

12. *Ctenochaetus strigosus* is recorded from the Society Islands. The young of this species in this island group and the Tuamotus (but not in the Hawaiian Islands) are bright yellow in life.

13. *Ctenochaetus hawaiiensis* is recorded from the Tuamotu Archipelago.

14. *Acanthurus olivaceus* is subspecifically distinct in the Marquesas Islands. Evidence of intergradation with the usual *olivaceus* form in the northern Tuamotus is presented.

15. The brown *Zebrasoma scopas* is common in the Societies and Tuamotus, but extensive collecting and underwater observation failed to reveal any of the yellow *Z. flavescens* in these islands.

16. The range of *Zebrasoma rostratum* is extended to include the Marquesas Islands, Caroline Atoll (10° S., 150° W.), and Palmyra in the Line Islands.

17. Two specimens of *Naso rigoletto*, known previously only from East Africa, were obtained in Tahiti, Society Islands.

18. The following surgeonfishes are here recorded from the Marquesas for the first time: *Acanthurus pyroferus*, *A. olivaceus*, *A. achilles*, *A. guttatus*, *A. nigroris*, *A. xanthopterus*, *A. bleekeri*, *Ctenochaetus strigosus*, and *Naso unicornis*.

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Two New Species of *Candacia* (Copepoda: Calanoida) from the Central Pacific, with Notes on Two Other Species[1]

GEORGE D. GRICE[2] and EVERET C. JONES[3]

DURING EXAMINATION of plankton samples collected from the central Pacific Ocean by the Honolulu Biological Laboratory (formerly Pacific Oceanic Fishery Investigations) of the U. S. Fish and Wildlife Service, two species of *Candacia* were found which appear to be undescribed. In addition to describing these two species we present evidence that *Candacia turgida* Wilson is a synonym of *C. truncata* (Dana). We also include a description and figures of *Candacia norvegica* (Boeck), a species apparently rare in the Pacific Ocean.

We wish to acknowledge the help of Dr. Thomas E. Bowman in loaning us type material from the U. S. National Museum, and that of Dr. Paul L. Illg for valuable suggestions during the preparation of the type material and the manuscript.

Candacia pofi new species
Figs. 1–21

LOCALITY AND MATERIALS: 1° 23′ S., 112° 46′ W. (U. S. Fish and Wildlife Service "Hugh M. Smith" cruise 31, station 75-3, Oct. 31, 1955, 200–140 m. depth of tow; 23 females and 6 males). Physical, oceanographic, and other data from this cruise have been published by King, Austin, and Doty (1957).

Type material of *Candacia pofi* has been deposited in the U. S. National Museum as follows: Female holotype (USNM 102730), male allotype (USNM 102731), 22 female paratypes and 5 male paratypes (USNM 102732).

MEASUREMENTS: Measurements were made from a dorsal view along a sagittal plane. The abdomen was supported by a plastic strip to reduce flexion. The copepod, stained with methyl blue and immersed in lactic acid, was mounted under a cover slip supported by plastic strips to avoid distortion due to pressure or a meniscus. The total length was measured from the anterior margin of the head to the ends of the caudal furca. The abdomen was measured from the anterior margin of the genital segment to the ends of the caudal furca. These measurements excluded the telescoped portions of the abdominal segments. The ratios of the lengths of the abdominal segments, however, include the telescoped portions as indicated by dotted lines in the figures. Pertinent measurements and ratios of the cephalothorax and abdomen of the holotype, allotype, 3 female paratypes, and 4 male paratypes are given in Table 1.

DESCRIPTION: In the adult female the cephalothorax (Fig. 1) is slender, being widest at the first thoracic segment. The posterior lateral angles of the thorax are produced into sharp symmetrical processes which reach to a line including 60 per cent of the length of the genital segment (Fig. 3). The genital segment (Fig. 3) is symmetrical in dorsal view, longer than wide and without lateral swellings or processes. The genital pore is situated on a very large protuberance which extends ventrad and caudad. In lateral view (Figs. 2, 4), the posterior margin of this protuberance is approximately continuous with the posterior margin of the genital segment. In ventral view (Fig. 5), the genital protuberance is round with a slight lip at the posterior margin. In the holotype, this lip is slightly asymmetrical. The second abdominal segment (Fig. 3) is asymmetrical in dorsal view, the right margin being convex and the left margin straight. The ventral surface is wrinkled and bears a low process which extends to the left as a lobe with a more or less crenulate margin.

[1] Contribution No. 131, Hawaii Marine Laboratory, University of Hawaii, with which one of the authors (G. D. G.) was associated. Manuscript received January 16, 1959.

[2] Fellow of the John Simon Guggenheim Memorial Foundation, 1958–59. Present address: Woods Hole Oceanographic Institution, Woods Hole, Massachusetts.

[3] Bureau of Commercial Fisheries, Biological Laboratory, Honolulu, Hawaii.

The dorsal surface of the anal segment (Fig. 3) bears a very prominent, broad bifurcate process pointing caudad. The posterior lateral surface of each of the diverging tubercles of this process has a patch of very fine teeth visible under 100× magnification. In the holotype, these tubercles appear to be slightly asymmetrical in size and in details of minute swellings and creases. Examination of paratype material indicates that there is variation in these details and also in the ventral lobe of the second abdominal segment.

The furcal rami (Fig. 3) are longer than wide. The outermost furcal setae are thick and originate high on the lateral margins of the rami. There is a small tooth dorsad of the origin of the middle major seta of each ramus.

The proximal seven segments of the first antennae are thickened. The first segment has three small spines, and segments 2 through 6 have small marginal spines (Fig. 6). It is probable that additional segments had spines which have been lost in the material at hand.

The second antennae are similar to those of other members of the genus. The exopod has six setae plus a minute one; the second endopodal segment is divided into two lobes, the external with six setae plus a minute one and the internal with five setae plus a minute one.

The exopod of the mandibular palpus has five setae; the endopod has six. The mandibular blades (Fig. 7) are composed of a large point and a basal tooth with three points decreasing in length mediad.

The first maxillae are best described by reference to Figure 8.

The second maxillae (Fig. 9) are large and have the form of maxillipeds. The basal segment is composed of four lobes. There is a single long seta on the first lobe with a minute seta at its base, two small setae on the internal margin of the second lobe, and one large spine with a short spine at its base on each of the third and fourth lobes. There are two long spines of about equal length on the second basipodal segment, and the proximal one has a minute spine at its base. Distad of the second basipodal segment are three very long, curved spines, the middle of which is the longest. Three very small bristles arise from the base of the distal spine.

The maxillipeds are reduced in length (Fig. 10). The first segment is about as long as the remaining segments combined and is 1.7 times the length of the second. There is a tubercle on the internal margin of the first segment near the proximal end and a single long seta just distad of the midpoint of that margin. Two slender setae, one twice the length of the other, arise from the junction of the first and second segments. At about the midpoint of the internal margin of the second segment, there is a patch of hair proximad of three setae. The distal end of this segment appears to receive the proximal end of the third so that the second and third each have three setae. Vervoort (1957), in describing *C. maxima*, attributes four setae to the second segment and two to the third. Giesbrecht (1892, pl. 21, figs. 26, 27) indicates that in *C. longimana* Claus the fourth seta is between the two segments but in *C. bispinosa* Claus it is on the third segment. This appendage is usually regarded as having little diagnostic value, but the origin of the fourth seta might add a distinguishing character. The fourth, fifth, and sixth segments have a pair of setae, the distal one in each pair being longer. Distad of the sixth segment are two long setae of almost equal length.

The lengths of the third exopodal segments of swimming feet 1 to 4 (Figs. 11–14) have the following relation to that of their respective terminal spines: 1:1, 2:1, 3:1, and 3:2.

The symmetrical fifth feet (Fig. 15) are long and slender, each ending in two sharp, smooth terminal fingers. The inner finger is about four times the length of the outer finger. There are two external spinous processes located at points about one-fourth and two-thirds of the segment length from the proximal end of the distal segment. There are no internal spines or setae. The penultimate segment bears a single seta, and the ratio of the length of that segment to that of the distal segment is 1:4.6.

Brown pigmentation in the female is restricted to the following structures: the fifteenth segment of the first antennae, the setae of the second antennae and the mandibular palpi, the second segment of the second max-

SCALES
0.1 MM. FIGS 3-6, 8, 9, 11-15, 18-21
0.05 MM. FIG. 7
1.0 MM. FIGS. 1, 2, 16, 17
0.05 MM. FIG. 10

TABLE 1
TOTAL LENGTHS, CEPHALOTHORAX–ABDOMEN RATIOS, AND ABDOMINAL SEGMENT RATIOS OF *Candacia pofi*

SPECIMENS	TOTAL LENGTH (mm.)	CEPHALOTHORAX–ABDOMEN RATIO	RELATIVE LENGTH OF ABDOMINAL SEGMENTS					
			1	2	3	4	5	Furca
Females								
Holotype	2.30	2.75:1	38	32	16	...	...	14 = 100
Paratype	2.41	2.64:1	42	30	16	...	...	12 = 100
Paratype	2.41	2.55:1	41	32	16	...	...	11 = 100
Paratype	2.36	2.75:1	39	29	17	...	...	15 = 100
Males								
Allotype	2.28	2.52:1	21	21	21	14	9	14 = 100
Paratype	2.21	2.61:1	21	21	21	14	9	14 = 100
Paratype	2.24	2.38:1	21	21	21	14	9	14 = 100
Paratype	2.23	2.54:1	...	...	...	...	...	... ...
Paratype	2.21	2.43:1	...	...	...	...	...	... ...

illae, the third exopodal segments of swimming feet 1 to 4, and the furcal setae.

The pertinent measurements and ratios of the adult males are presented in Table 1. The posterior lateral angles of the male cephalothorax (Fig. 16) are produced into asymmetrical processes. The left is sharp and reaches to the posterior margin of the genital segment. The right process (Fig. 18) is thick and slightly curved inward and reaches to a line including one-quarter of the length of the second abdominal segment. In lateral view (Figs. 17, 19), this right process is thick and truncate with a convex dorsal margin and a concave ventral margin.

The male genital segment (Fig. 18) is asymmetrical with a rounded swelling tipped with a small button on the right side. In lateral view (Fig. 19) the swelling appears as two or three concentric, incomplete circles. The left posterior margin of the genital segment is broken by the genital opening. In the allotype, a canal is visible from the genital opening to a spermatophore (Fig. 18).

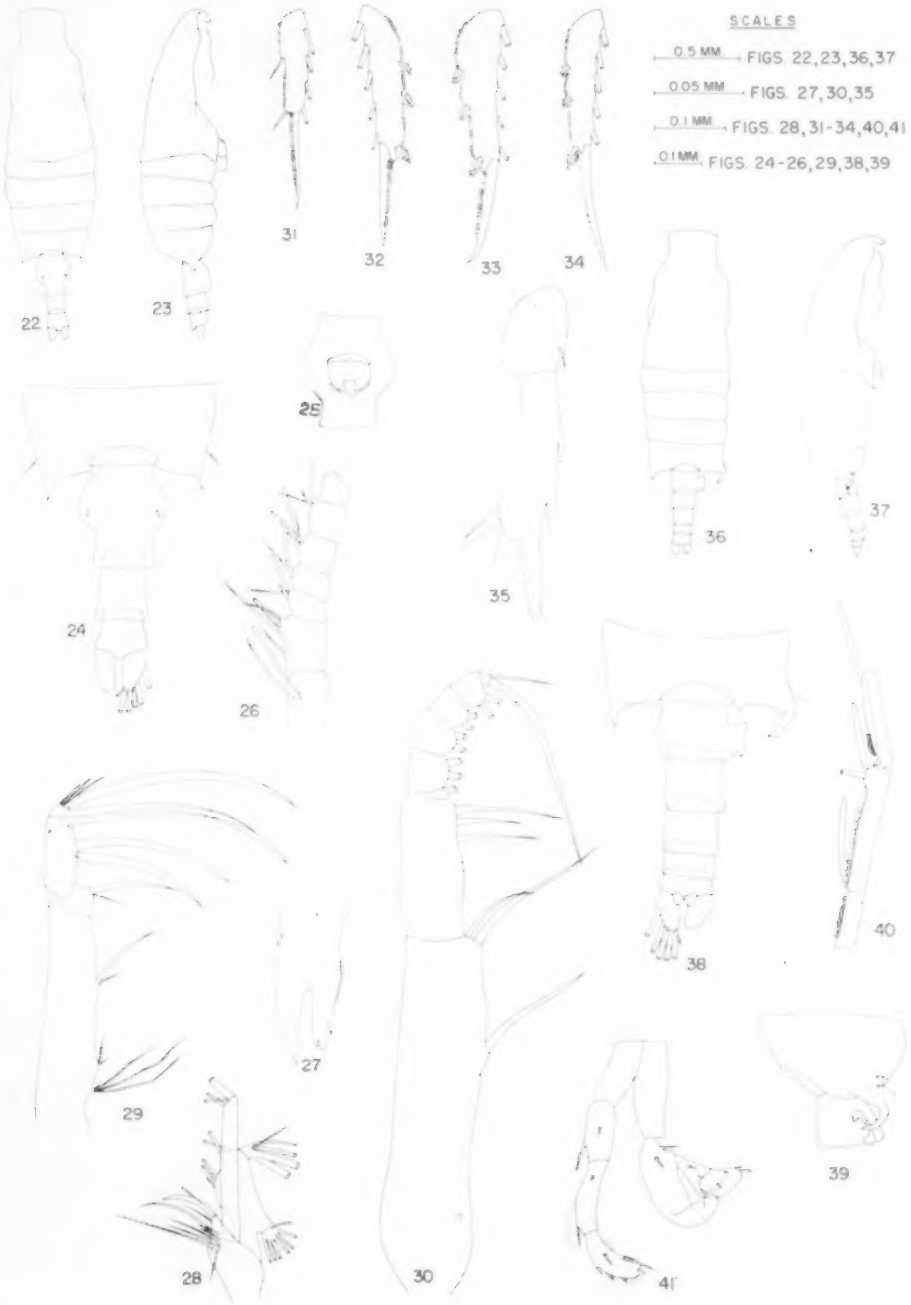
The geniculate right antenna (Fig. 20) is armed with coarse, unequal pigmented teeth on segment 18, fine pectination on segment 17 extending onto the anterior margin of a distal spinous process, and very fine pectination on segment 19. Segments 17, 18, 19, and 20 are separate.

The right fifth foot (Fig. 21) is chelate with the tip of the distal segment reaching slightly beyond that of the penultimate segment. The terminal spine is turned flat against the surface of the distal segment. The left fifth foot is broad and ends in a spatulate segment (Fig. 21).

Pigmentation is similar to that of the female. In addition, the geniculate portions of the right first antenna are heavily pigmented. There is no pigmentation on the right thoracic process or the genital segment.

REMARKS: The female of *C. pofi* resembles *C. cheirura* Cleve (as described by Farran, 1929) in having ventral protuberances on the genital and second abdominal segments, and thick ex-

FIGS. 1–21. *Candacia pofi* n. sp. 1, female, dorsal view; 2, female, lateral view; 3, fourth and fifth thoracic segments and abdomen, dorsal view, female; 4, fourth and fifth thoracic segments and abdomen, lateral view, female; 5, abdomen, ventral view, female; 6, proximal 10 segments of first antenna, female; 7, mandibular blade, female; 8, first maxilla, female; 9, second maxilla, female; 10, maxilliped, female; 11, third exopodal segment of first foot, female; 12, third exopodal segment of second foot, female; 13, third exopodal segment of third foot, female; 14, third exopodal segment of fourth foot, female; 15, fifth foot, female; 16, male, dorsal view; 17, male, lateral view; 18, fourth and fifth thoracic segments and abdomen, dorsal view, male; 19, fourth and fifth thoracic segments and abdomen, lateral view, male; 20, segments 13 through 19, right first antenna, male; 21, fifth feet, male. Figures 1–12 and 15 drawn from holotype; Figures 13 and 14 from paratype. Figures 16–19 and 21 drawn from allotype; Figure 20 from paratype.


SCALES
0.5 MM FIGS. 22,23,36,37
0.05 MM FIGS. 27,30,35
0.1 MM FIGS. 28,31-34,40,41
0.1 MM FIGS. 24-26,29,38,39
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ternal furcal setae. It can be distinguished from *C. cheirura* by the asymmetry of the abdomen in dorsal view and by the presence of dorsal tubercles on the anal segment. The female resembles *C. armata* Boeck (as described by G. O. Sars, 1903) in having an asymmetrical second abdominal segment. It can be distinguished from this species by the extremely large genital protuberance, the ventral lobe of the second abdominal segment extending to the left rather than to the right, the dorsal tubercles on the anal segment, and details of the fifth feet.

The geniculate antenna of the male *C. pofi* resembles that of *C. armata* Boeck (as described by Sars, 1903), *C. bradyi* and *C. discaudata* A. Scott, *C. bipinnata* Giesbrecht, and *C. cheirura* Cleve in having segments 17, 18, 19, and 20 separate and in having coarse, unequal pigmented teeth on segment 18. *C. pofi* can be distinguished from *C. bradyi* and *C. discaudata* by the produced right thoracic process. It can be distinguished from *C. armata, C. bipinnata,* and *C. cheirura* by the low, rounded genital process in lieu of the sharp spinous process in those species. The name of this species is derived from Pacific Oceanic Fishery Investigations.

Candacia guggenheimi new species
Figs. 22–41

LOCALITIES AND MATERIALS: 26° 25.2′ N., 155° 03.0′ W. (U. S. Fish and Wildlife Service "Hugh M. Smith" cruise 25, sta. 33, Feb. 10, 1954, 200–0 m. depth of tow, 2 females, 4 males); 32° 33′ N., 148° 51.5′ W. ("Hugh M. Smith" cruise 25, sta. 53, Feb. 22, 1954, 200–0 m. depth of tow, 1 male); 23° 56′ N., 157° 31′ W. ("Hugh M. Smith" cruise 30, sta. 112-1, Aug. 27, 1955, 140–0 m. depth of tow, 1 female); 21° 55′ N., 158° 08′ W. ("Hugh M. Smith" cruise 32, sta. 26, Feb. 5, 1956, 200–140 m. depth of tow, 1 female, 1 male); 0° 00′, 149° 38′ W. ("Hugh M. Smith" cruise 47, sta. 29, Oct. 27, 1958, 500 m. depth of tow, 1 female). This species has also been observed in samples collected at the following stations on "Hugh M. Smith" cruise 25 (all 200–0 m. collections): 21° 36.5′ N., 159° 00′ W. (sta. 2, Jan. 16, 1954); 33° 55.7′ N., 164° 58.5′ W. (sta. 11, Jan. 22, 1954); 26° 31′ N., 160° 00′ W. (sta. 26, Jan. 30, 1954); 22° 03.7′ N., 158° 40′ W. (sta. 29, Feb. 1, 1954); 29° 32′ N., 155° 04.8′ W. (sta. 35, Feb. 12, 1954); 32° 30′ N., 154° 59′ W. (sta. 37, Feb. 13, 1954). Physical, oceanographic, and other data for cruise 25 have been summarized by McGary and Stroup (1956) and that for cruise 30 by McGary, Jones, and Austin (1956).

Type material of *C. guggenheimi* has been deposited in the U. S. National Museum. A female from cruise 25, sta. 33, was selected as the holotype (USNM 102733). A male from this station was designated the allotype (USNM 102734). Paratypes are as follows: 1 female, 3 males, cruise 25, sta. 33 (USNM 102735); 1 male, cruise 25, sta. 53 (USNM 102736); 1 female, cruise 30, sta. 112-1 (USNM 102737); 1 female, 1 male, cruise 32, sta. 26 (USNM 102738); 1 female, cruise 47, sta. 29 (USNM 102739).

MEASUREMENTS: All measurements were made in the method described for the preceding species. The total length of five adult females ranges from 1.94 to 2.06 mm. The lengths and cephalothorax–abdomen ratios, based on three of these individuals are: holotype 2.01 mm., 2.9:1; paratypes 1.96 mm., 2.8:1; 2.04 mm., 3.1:1.

The total length of six adult males varies from 1.90 to 2.00 mm. These lengths and the

FIGS. 22–41. *Candacia guggenheimi* n. sp. 22, female, dorsal view; 23, female, lateral view; 24, fourth and fifth thoracic segments and abdomen, dorsal view, female; 25, genital segment, ventral view, female; 26, proximal seven segments of first antenna, female; 27, mandibular blade, female; 28, first maxilla, female; 29, second maxilla, female; 30, maxilliped, female; 31, third exopodal segment of first foot, female; 32, third exopodal segment of second foot, female; 33, third exopodal segment of third foot, female; 34, third exopodal segment of fourth foot, female; 35, fifth foot, female; 36, male, dorsal view; 37, male, lateral view; 38, fourth and fifth thoracic segments and abdomen, dorsal view, male; 39, fourth and fifth thoracic segments and genital segment, lateral view, male; 40, segments 17 through 19, right first antenna, male; 41, fifth feet, male. Figures 22, 23, 27, and 34 drawn from paratype; Figures 24–26, 28–33, and 35 drawn from holotype. Figures 36–39 and 41 drawn from allotype; Figure 40 drawn from paratype.

cephalothorax–abdomen ratios, based on four of these, are: allotype 1.90 mm., 2.91:1; paratypes 1.92 mm., 2.9:1; 1.94 mm., 2.7:1; 2.00 mm., 2.7:1.

DESCRIPTION: The general shape of the adult female is similar to other species of the genus *Candacia*. The head is truncate in dorsal view; thoracic segments 4 and 5 are fused and produced posteriorly into two symmetrical points (Fig. 22). In lateral view (Fig. 23), a small hump is visible on the dorsal surface at the junction of the head and first thoracic segment.

The genital segment is slightly asymmetrical; the lateral swelling on the left side is smaller and somewhat more expanded than that on the right side (Figs. 24, 25). A single dorsal spine is present on each swelling. The abdominal segments and furca have the following proportions (based on holotype): 40, 26, 19, 15 = 100.

The first antennae, when held against the body, reach to about the tips of the furcal rami. The proximal part of the antenna is thickened and consists of seven segments (Fig. 26). Segments 1 through 6 and 8 through 12 have one spine. There are indications that additional segments are furnished with a spine but no perfect antennae were present among the specimens examined.

The second antennae are similar to those of other species of *Candacia*. Basipodal segments 1 and 2 have one seta. Segment 2 of the endopod ends in two lobes. The outer lobe has six large and one small setae. The inner lobe has five large and one small setae and one minute seta proximad of the small one.

The exopod of the mandible apparently consists of four segments, the first three of which are furnished with a single seta. The terminal segment has two setae. The endopod is composed of one segment which is provided with six setae. The basal tooth of the mandible is furnished with two subequal points and a marginal point (Fig. 27).

The first maxillae are best described by reference to Figure 28.

The second maxillae are of large size (Fig. 29). The basal segment has four lobes. There are three long and one very short setae on the first lobe, one long and one short seta on the second lobe, one long and one short spine on the third lobe, and one long and one short spine on the fourth lobe. The second basipod segment has two subequal spines, the proximal one has a minute spine at its base. The endopod is furnished with three spines, the middle of which is slightly longest. In addition there are three bristles on the terminal part of the endopod.

The maxillipeds (Fig. 30) are small. The first basal segment is more than twice as long as the second basal segment. The former has one seta at a point about two-thirds of the segment length from the proximal end and two setae on the distolateral corner. The second basal segment is furnished with three unequal setae and one other seta on the apparent apex. Hair is present on the internal margin of this segment. The five endopodal segments are each furnished with one long and one short seta. The long seta on the terminal segment is somewhat longer than those on the other endopodal segments.

The third exopodal segments of swimming feet 1 to 4 are shown in Figures 31–34. The relative lengths of these segments to their respective terminal spines are as follows (based on several specimens): 1:1, 1:0.8 (estimate), 1:0.6, and 1:1.

The fifth feet are symmetrical and each terminates in one long stout finger and one short spinous process (Fig. 35). The former is about three times longer than the latter. The finger has several rounded serrations distally, and the spinous process is finely serrate. The external margin of the segment has two spinous processes. The internal margin bears two subequal setae in all observed specimens except one ("Hugh M. Smith" cruise 47, sta. 29-1) which has three internal setae on one foot.

The following appendages of the preserved holotype are pigmented: the distal 18 segments of the first antennae, the distal spinelike claw on the first inner lobe of the first maxillae, portions of the first basipod segment and the distal five spines of the second maxillae, basipodal segments 1 and 2 of the first four pairs of swimming feet, and the terminal finger and spinous process of the fifth pair of feet. The female collected on "Hugh M. Smith" cruise 47, sta. 29, has additional pigmentation as follows: the distal 20 segments of first antennae, the spines

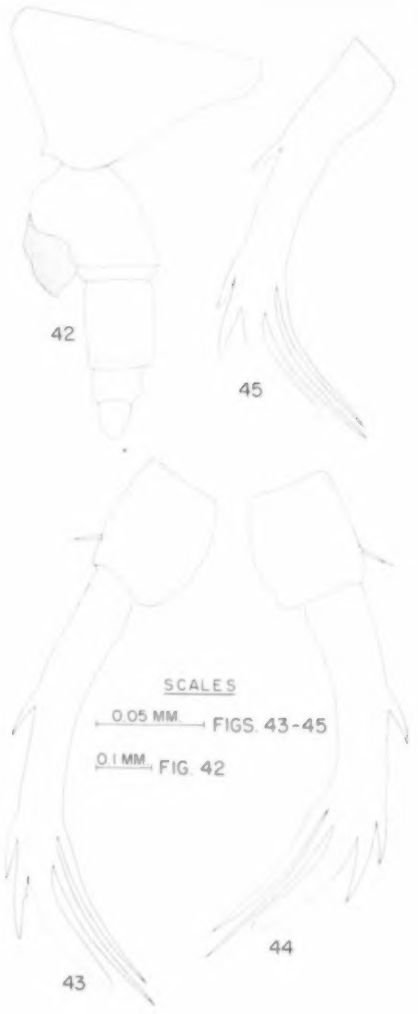
on lobes 3 and 4 of the second maxillae, much of both rami of swimming feet 1 to 4 including several setae on the second and third exopodal segments and second endopodal segment, and the first basipodal segment of the fifth pair of feet.

The adult male (Figs. 36, 37) is slightly smaller than the female. The right posterior lateral process of the fifth thoracic segment is produced posteriorly and curved inward in dorsal view (Fig. 38). It reaches to the middle of the protrusion on the genital segment. In lateral view, the thoracic process has a decided upward bend (Fig. 39). The genital segment has a bilobed protrusion arising from near the posterior end of the right margin (Fig. 38). The abdominal segments and furca have the following ratios (based on three specimens): 22, 24, 20, 13, 9, 12 = 100.

Segments 17, 18, 19, and 20 of the right first antenna (Fig. 40) are separate, with 17, 18, and 19 toothed. The nearly uniform teeth on segment 18 are coarser than those on segments 17 and 19. The fifth feet are shown in Figure 41.

The following body parts and appendages of the male are pigmented (based on examination of several specimens): segments 17 to 25 of the right antenna, the distal 17 segments of the left antenna, the process on the right corner of the fifth thoracic segment, the clawlike spine on the distal part of the first inner lobe of the first maxillae, portions of the first basipod and spines on lobes 3 and 4 and the five large distal spines of the second maxillae, basipodal segments 1 and 2 of swimming feet 1 to 4.

REMARKS: The female of *C. guggenheimi* superficially resembles *C. longimana* Claus. The spines on the dorsal surface of the genital segment, the structure of the fifth pair of feet, and the somewhat smaller size of this species readily distinguish it from *C. longimana*. The bilobed protrusion on the genital segment and the structure of the fifth feet serve to distinguish the male. This species is named for the late Simon Guggenheim, one of the founders of the John Simon Guggenheim Memorial Foundation.



FIGS. 42–45. *Candacia truncata* (Dana). 42, fourth and fifth thoracic segments and abdomen, left lateral view, female, showing cement mass attached to genital segment; 43, 44, unlike fifth feet, female, from same specimen; 45, fifth foot, female, with serrated external spinous processes, from another specimen.

NOTES ON TWO OTHER SPECIES

Candacia truncata (Dana)
Figs. 42–45

Candace truncata Dana, 1849, Proc. Amer. Acad. Arts Sci., 2: 24.
Candacia truncata Giesbrecht and Schmeil, 1898, Das Tierreich, 6, p. 130; auct.
Candacia turgida Wilson, 1950, U. S. Natl. Mus. Bul. 100, 14(4): 183–184. New synonomy.

In the course of examining plankton samples we have encountered numerous individuals of a species which appears to agree with the description of *C. turgida* Wilson (1950). We believe, however, that these specimens, as well as *C. turgida*, are identical with *C. truncata* (Dana).

The pigmented process on the ventral side of the female genital segment (shaded portion of Fig. 42), which Wilson considered to be a protrusion of that segment, appears to be a mass of cement associated with a spermatophore. In most of the samples examined there were some females with this mass and others without. Furthermore, the mass can be removed quite easily with a needle. Tanaka (1935) presented a figure of a female *C. truncata* showing such a mass adhering to the genital segment.

Wilson's figure of the female fifth feet (1950: pl. 22, fig. 308) of his *C. turgida* apparently is not complete in detail. Dr. Thomas E. Bowman has kindly sent us a sketch of the fifth feet from one of the syntypes of this species. His sketch and the numerous fifth feet examined from our material agree in the structure of the large terminal finger. The external margin of this finger in all specimens examined and in Dr. Bowman's sketch is finely serrate along most of its length. The distolateral and two external spinous processes are, however, somewhat variable. In some specimens the distolateral spinous process has one or two relatively large teeth on the internal margin as figured by Giesbrecht (1892). One has a single external tooth opposite two internal ones; another has seven small internal teeth. In some specimens the feet are asymmetrical, being unequal in length and with unlike dentition on the distolateral spinous process. One specimen has four teeth on one foot and two on the other. In yet another, this process is toothed on one foot and smooth on the other. Figures 43–45 show some of the variations of the fifth feet of the female *C. truncata* from the central Pacific. Typical males of *C. truncata* have also been observed in our collections. Specimens of this species were obtained in the following localities: 22° 03.7′ N., 158° 40′ W. ("Hugh M. Smith" cruise 25, sta. 29, Feb. 1, 1954, 200–0 m. depth of tow); 0° 00′, 149° 36′ W. ("Hugh M. Smith" cruise 47, sta. 30, Oct. 27, 1958, surface collection). Seven females from 23° 55′ N., 157° 31′ W. ("Hugh M. Smith" cruise 30, sta. 112-2, Aug. 27, 1955, 49 m. depth of tow) have been deposited in the U. S. National Museum (USNM 102740).

Candacia norvegica (Boeck)
Figs. 46–65

The distribution of *Candacia norvegica* (Boeck) in the North Atlantic has been summarized by Farran (1948). Sewell (1932) described a variety *tropica* from the Indian Ocean. In his reports on the Carnegie and Albatross collections, Wilson (1942, 1950) recorded *C. norvegica* from many stations in the tropical and temperate Pacific Ocean. In a

FIGS. 46–65. *Candacia norvegica* (Boeck). Figures 46–62 refer to Pacific specimens; Figures 63–65 to Atlantic specimen. 46, female, lateral view; 47, abdomen, dorsal view, female; 48, lateral view of left genital spinous process; 49, lateral view of right genital spinous process; 50, 51, mandibular blades from one individual female, showing unlike basal teeth; 52, first maxilla, female; 53, second maxilla, female; 54, fifth feet, female, with two external spinous processes on each foot; 55, fifth feet, female showing three external spinous processes on one foot and two on the other; 56, male. dorsal view; 57, male, lateral view; 58, fourth and fifth thoracic segments and abdomen, dorsal view, male; 59, genital segment, ventral view, male; 60, fourth and fifth thoracic segments and genital segment, right lateral oblique view, male; 61, segments 17 through 19, right first antenna, male; 62, fifth feet, male; 63, abdomen, dorsal view, female; 64, left genital spinous process; 65, right genital spinous process. Figures 47–49 and 54 are from Pacific female 2.96 mm. total length; all others of Pacific female are from specimen 2.80 mm. total length.

SCALES
1.0 MM FIGS. 46,56,57
0.05 MM FIGS. 48-51,64,65
0.1 MM FIGS. 52,54,55,60-62
0.1 MM FIGS. 47,53,58,59,63
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TABLE 2
COMPARISON OF FEMALE *Candacia norvegica* FROM GEORGES BANK, THE PACIFIC, AND VARIETY *tropica*

SOURCE	TOTAL LENGTH* (mm.)	CEPHALOTHORAX–ABDOMEN RATIO*	ABDOMEN RATIO = 100 SEGMENT NUMBER			
			1	2	3	Furca
Georges Bank (USNM)	3.24	2.89:1	45	24	18	13
Pacific	2.96	2.66:1	45	24	17	14
Pacific	2.80	2.83:1	44	22	19	15
Variety *tropica* (Sewell, 1932)†	2.28	2.92:1	43	25	19	13

* Includes telescoped portion of abdominal segments of the specimens from Georges Bank and from the Pacific. Sewell's data used for *tropica*.

† Sewell apparently reversed the figures for the ratio of the anal segment and furca. Measurement of his figure of the abdomen shows that the length of the anal segment exceeds that of the furca.

recent paper, Fleminger and Bowman (1956) have reported that Wilson's determinations were incorrect and that *C. norvegica* was not present in any of the Carnegie and Albatross material in the U. S. National Museum. The only other mention of this species from the Pacific appears in Tanaka's (1953) list from the Izu region off southern Japan. Because no description or figures have been given of Pacific specimens and because of the apparent rarity of the species in that ocean, we are including a description based on two females and one male collected in the central North Pacific. These specimens were collected at 37° 43.9′ N., 165° 0.5′ W. ("Hugh M. Smith" cruise 25, sta. 13, Jan. 24, 1954, 200–0 m. depth of tow, 2 females and 1 male) and have been deposited in the U. S. National Museum (USNM 102741).

We have compared our specimens with Atlantic *C. norvegica* collected south of Georges Bank (northwest Atlantic) and loaned to us by the U. S. National Museum, with Sewell's description of *tropica*, and with Sars' (1903) redescription of *C. norvegica* based on specimens from the Norwegian Sea. Differences in the details of the lateral spines of the female genital segment were found. Sars implied in his description that these spines are simple and single pointed. Variety *tropica* Sewell is stated to have bifid spines on both sides. Our Pacific specimens agree with *tropica* in this respect, but the spines are somewhat smaller (Figs. 48, 49). The Georges Bank specimen examined by us has a slightly bifid tip on the left spine and a simple spine on the right (Fig. 64). Furthermore, Sars stated that the genital segment is perfectly symmetrical, but in the specimens from the Pacific (Fig. 47) and Georges Bank (Fig. 63) and in *tropica*, the left spine is larger than the right. We believe that the size and detail of these spines is variable and may be of little diagnostic value. Table 2 gives the total length, cephalothorax–abdomen ratio, and abdominal segment ratios of the specimen from Georges Bank, Pacific specimens, and Sewell's variety *tropica*.

The structure of the female fifth feet presents some variation among specimens from the Pacific and Georges Bank, Sewell's *tropica*, and Sars' description. Sewell stated that the fifth feet of *tropica* were unlike *norvegica* in that there are two rather than three "spines" on the outer margin of the distal segment, but Sars (1903) mentioned that this margin may have two or three small "denticles." Of our two Pacific specimens, one has two spinous processes on each foot (Fig. 54), and the other has two on one foot and three on the other (Fig. 55). The Georges Bank specimen has two outer spinous processes on each foot. It appears that this is a variable characteristic. In *tropica* the two terminal fingers of the fifth feet are equal, but in all others examined or described the length of the outer is about twice that of the inner finger.

Sars stated that the points on the corners of the fifth thoracic segment diverge in dorsal view, but in all other specimens and descriptions examined by us these points point straight caudad.

The male from the Pacific (Figs. 56–62) agrees closely with the Georges Bank specimen and with the description given by Sars. The total length of our specimen is 2.68 mm. and that of the Atlantic specimen is 3.23 mm.

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Contributions to the Knowledge of the Alpheid Shrimp of the Pacific Ocean

Part VI. *Prionalpheus*, a New Genus of the Alpheidae[1]

ALBERT H. BANNER and DORA MAY BANNER[2]

IN THE EXTENSIVE collections of shrimp upon which this series of papers is based, there are three fragmentary specimens in which the mouth parts are entirely unlike those of any other genus of the family Alpheidae. These are of two species but, because of the fragmentary condition of the specimens, only one of the species is named. The specimens were collected in Fiji and the Society Islands while the senior author was there under a grant from the Bernice P. Bishop Museum, Honolulu. The study has been supported by grants from the National Science Foundation (NSF–G 1754 and NSF–G 3863).

Prionalpheus gen. nov.

DIAGNOSIS: Body form usual, similar to *Alpheopsis;* rostrum present and small; supra-, extra-, and infracorneal teeth lacking; anterior carapace projecting to cover corneas from dorsal and lateral view, flat, not inflated to form orbital hoods; antennules and antennae normal for family; mandibles without a trace of molar process, incisor process greatly expanded and consisting of five strong teeth, the most anterior tooth of left mandible developed as an awl-shaped process that slides within almost closed tube formed by corresponding portion of right mandible; maxillulae with middle lobe moderately or greatly expanded, inner lobe bearing strong spines; maxillae reduced in size, endites greatly reduced, palp present, scaphognathite relatively small and narrow; first maxilliped with endite large and rounded, endopod without apparent segmentation, exopod well developed but without any basal exite, epipodites present; second maxilliped with basal article of endopod apparently united with basipodite and large, next article somewhat to greatly reduced, penultimate article not greatly expanded and ultimate article rounded in outline rather than short and laterally expanded; third maxillipeds not markedly different from those of other genera; only one cheliped known, similar in form to those of *Alpheopsis equalis* Coutière; second legs with carpus divided into three or four articles; following legs slender, elongate with biunguiculate dactylus; pleura of sixth abdominal somite articulated; telson and uropods normal; no anal tubercles; branchial formula apparently including five pleurobranchs, no arthrobranchs, and epipodites only on first and second maxilliped.

TYPE SPECIES: *Prionalpheus triarticulatus*, described below.

DISCUSSION: Even without both chelae of the first pair, there can be no doubt that this genus belongs to the family Alpheidae. This is shown by the development of the sole chela on the first walking legs and the chelate second legs with a multiarticulate carpus, by the whole body form, by the development of the carapace to cover the orbits of the eyes, by the development of the antennules and antennae, as well as by less important characteristics like the form of the third legs, the development of articulated pleura of the sixth abdominal segment, and the form of the telson and uropods. If it were not for the unique development of the mouth parts, these species would fall into the genus *Alpheopsis* without modification of the generic description.

However, no mouth parts like these have been described for any species of any genus of the family. In Coutière's thesis (1899: 153–173) the mouth parts of the members of the family were shown to have little variation, with the possible exception of the third maxilliped. No subsequent publication has shown any greater differences in the inner mouth parts, although

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Chace did erect a new genus *Pomognathus* (1937: 124, fig. 5) on the basis of a species with an expanded third maxilliped. In *Prionalpheus* the differences lie principally in the overdevelopment of the incisor process portion of the mandibles, with the corresponding loss of the palp and molar portion, and in the seemingly primitive condition of the second maxilliped, which, although it has coalescence of some of the articles, assumes a form more reminiscent of the maxilliped of Mysidacea than those of most other Decapoda. The development of the maxillulae differs in the two species, and the modification of the maxillae and of the first and third maxillipeds are not as striking. The inclusion of this genus within the family Alpheidae will necessitate changes in its definition as given by Coutière ("Mandibles toujours profondément bipartites, 'palpe' à deux articles. . . ." 1899: 322).

As stated above, except for the development of the mouth parts, this genus is most similar to *Alpheopsis* within the family. Of course, without the chelae it is difficult to decide where its affinities lie, but even if they were present and similar to those of *Alpheopsis* as they are expected to be, it would still be difficult to assign this genus to any phylogenetic scheme for the family. It is generally accepted that *Athanas* is the most unmodified genus, and *Alpheus* and *Synalpheus* the most highly modified, on the basis of both the orbital hoods and development of the large chela; such a scheme would leave *Alpheopsis* in an intermediate position. However, *Prionalpheus*, intermediate in most characteristics, is not intermediate in the modification of the mouth parts.

The species of *Alpheopsis* available in the collection, including *Alpheopsis equalis* Coutière, *A. diabolus* Banner, and *A. tetrarthri* Banner, have been re-examined to determine if they have this modification of mouth parts. They do not. However, two species described by Coutière, *A. idiocarpus* and *A. fissipes* (1908:4), should also be re-examined; *A. idiocarpus* especially appears to be similar to *P. triarticulatus*.

It is unfortunate that the specimens were so few in number, because a number of characteristics should be investigated more thoroughly by dissection. For example, the origin of the peculiar tooth on the ventral side of the body at the base of the antennules should be studied; the branchial formula should be determined more carefully; the mouth parts of the right side should be compared to those of the left. With only three specimens representing two species, it was decided to leave the specimens intact for future workers.

Little can be said of the distribution of these species. All three were collected from the usual collecting site for snapping shrimp, the reef flat and the outer portion of the reef, in Fiji and Tahiti. No special niche or commensal association was noted for them, yet these three specimens were the only ones found in all of the collecting trips to similar habitats in these and other islands, collections that produced about eight thousand specimens. Presumably, these species must have special environmental requirements, but what the requirements may be we cannot say.

The generic name is derived from the Greek, *prionos*, meaning "saw"; the gender is masculine, as it is in *Alpheus*.

KEY TO THE SPECIES

Carpus of second legs with three articles; only scattered setae on terminal article of third maxillipeds, these not reaching over half the length of that article..... *Prionalpheus triarticulatus*

Carpus of second legs with four articles; terminal article of third maxillipeds bearing numerous setae equal in length to that article..... *Prionalpheus* species

Prionalpheus triarticulatus sp. nov.
Fig. 1

TYPE AND ONLY SPECIMEN: A 10.7 mm. nonovigerous female (3.9 mm. carapace length) collected in middle of reef flat on fringing reef, Korolevu, Vitilevu, Fiji, by senior author, 17 March 1954 (BF-13).

DESCRIPTION: Rostrum triangular, base demarked from adjacent margin of carapace, tip acute, reaching to end of first antennular article, and bearing four short setae; dorsal surface with slight carina. Anterior carapace obscuring eyes from dorsal and lateral views, but not form-

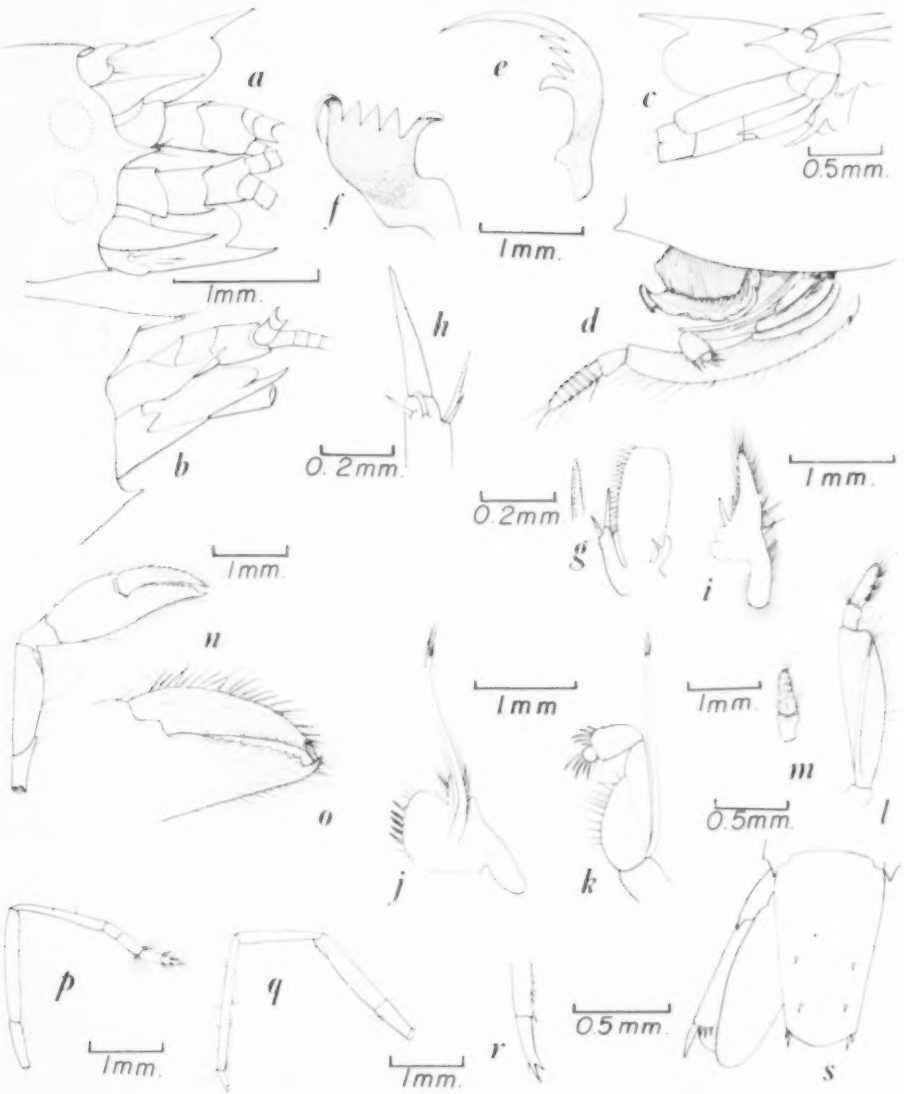

FIG. 1. *Prionalpheus triarticulatus* Banner. *a, b,* Anterior body region; *c,* base of antenna and antennules, in situ, ventral view; *d,* mouth parts of right side, medial view, showing groove on anterior end of mandible; *e,* left mandible, posterior view; *f,* left mandible, medial view; *g,* first maxilla, with enlargement of teeth on bristle; *h,* first maxilla, inner lobe, side opposite of *g*; *i,* second maxilla; *j, k, l,* first, second, and third maxillipeds; *m,* distal articles, inner face, third maxilliped; *n,* chelipeds, lateral view; *o,* fingers of chela; *p,* second legs; *q,* third legs; *r,* third leg of dactylus; *s,* telson and uropods.

ing swollen orbital hoods; without trace of ocular teeth; pterygostomial tooth produced and acute.

Basal articles of antennules short and heavy, with second article slightly broader than long; lateral spine of stylocerite strong, with tip reaching slightly beyond end of second antennular article. Ventral lateral tooth of basicerite heavy, acute, and curving under scaphocerite; superior lateral margin of basicerite projecting as a rounded lobe; scaphocerite with strong lateral spine, slightly curved towards tip, and reaching beyond end of antennular peduncle, squamous portion broad and anteriorly rounded, reaching to end of antennular peduncle; carpocerite equal in length to antennular peduncle. Either basal article of antennules or of antennae, or sclerite at their bases on ventral side of head bearing a sharp, acute tooth (see Fig. 1*c*).

Mouth parts protrudent and conspicuous in lateral view. Mandible large, curved distally and flattened laterally, bearing five teeth; posterior tooth acute, longer than middle teeth and curved; three middle teeth strong, acute, and of equal size; anterior tooth of left mandible awl-shaped, curved, almost 4 times the length of middle teeth and fitting into almost closed groove developed by corresponding tooth of right mandible; no trace of palp or *pars molaris*. Maxillulae with middle lobe greatly expanded, 2.2 times as long as broad, exceeding the inner lobe by 0.7 of its length, distally truncate with rounded corners, and bearing two series of setae on inner margin; inner lobe short, obliquely truncate, and bearing strong terminal spine almost as long as article and four other shorter spines, one curved; outer lobe smaller than inner and bearing a single weak spine. Maxillae reduced in size with total length of scaphognathite equal to length of maxillule; endites reduced to small lobes; palp without segments and bearing only few setae; setiferous scaphognathite narrow, with posterior lobe only 2 times as long as broad. First maxilliped with endite rounded, solitary (unless basal endites were lost in dissection), bearing four strong articulated spines and a few setae; endopod with no apparent segmentation, bearing few setae; exopod well developed; epipodite well developed, lobe-like, rounded. Second maxilliped apparently with only four articles distal to articulation of exopod; basal article of endopod with maximum length twice the breadth, inner margin bearing strong spines; next article with maximum length 0.7 that of basal article; penultimate article broader but shorter than preceding article, bearing setae; ultimate article half as broad and one-quarter as long as penultimate, bearing five strong articulated spines. Third maxillipeds normal for family, with ultimate article twice length of penultimate, 0.3 length of basal article, and bearing few short scattered setae along margins.

Only one of first pair of legs present. Ischium 0.3 length of merus; merus 4 times as long as broad, unarmed, bearing few scattered setae; carpus somewhat cyathiform, distally expanded to accommodate base of propodus; palm slightly shorter than fingers, 0.7 as long as broad, somewhat compressed; fingers heavy, fixed finger bearing fine serrations, dactylus with straight cutting edge, free margin armed with setiferous bristles; tips of fingers crossing.

Second legs with merus 7 times as long as broad; three articles of carpus with ratio 10:2:3, first article 0.8 as long as merus, twice as wide distally as proximally; fingers and palm of chela subequal, together 1.4 times as long as distal article.

Third legs with ischium 0.4 length of merus, bearing three setae; merus 5 times as long as broad, unarmed; carpus 0.9 as long as merus, also unarmed; propodus 1.4 times length of merus, about 15 times as long as broad, armed with short, very fine spines and setae along inferior margin; dactylus biunguiculate, with inferior unguis the heavier and shorter.

Telson 2.8 times as long as broad distally, 1.5 times as broad proximally as distally, sides with uniform taper, tip broadly arcuate, dorsal and terminal spinules small. Uropods narrow; tooth on proximal article small; distal tooth on outer uropod heavy, flanked by three smaller teeth.

DISCUSSION: The origin of the spine on the ventral side of head could not be ascertained without dissections which would ruin the type

specimen. It appears to arise from an inner portion of the base of the antennae.

This species will be contrasted to *Prionalpheus* species under that form. It is superficially similar to *Alpheopsis idiocarpus* Coutière, a species that may be found to be in this genus when it is re-examined; the two species differ, however, even if the mouth parts should be found to be similar, in the biunguiculation of the dactylus of the third leg. *Alpheopsis fissipes* Coutière, which may also be found to belong in this genus, differs in the number of articulations of the carpus of the second legs.

The specific name refers to the number of articles of the carpus of the second leg.

Prionalpheus sp.
Fig. 2

LOCALITIES: 1 female, nonovigerous, carapace length 2.8 mm., total length 5.6 mm., from Arue, Tahiti, in dead coral heads 5–10 ft. deep (BD-3); 1 ovigerous female, carapace length 3.7 mm., total length 10.6 mm., from outer edge of fringing reef at Korolevu, Vitilevu, Fiji (BF-16); both collected by senior author. Tahitian specimen with one second and one third leg intact; Fijian specimen with only second legs intact.

DESCRIPTION: Base of rostrum not demarked from curvature of anterior margin of carapace, tip of rostrum reaching to middle of first antennular article and bearing four setae; pterygostomial angle somewhat produced and acute, but not projecting as a definite tooth.

Antennular peduncle short and heavy, with second article about as long as broad; stylocerite reaching almost to end of second antennular article; outer flagellum bearing numerous heavy, but not stiff, setae. Ventral lateral spine of basicerite acute but shorter than that of *P. triarticulatus;* dorsal lateral lobe present; lateral spine of scaphocerite reaching to middle of third antennular article, rounded edge of squamous portion to end of second article; carpocerite reaching to end of antennular peduncle. No ventral spine anterior to labrum at bases of antennules or antennae.

Left mandibles similar to that of *P. triarticulatus* except anterior awl-shaped tooth only twice as long as adjacent tooth, and posterior tooth not acute but rounded; anterior process of left mandible fitting into corresponding groove of right mandible. Maxillulae of more normal form, as shown in Figure 2*e*; inner lobe bearing numerous strong, hooked setae. Maxillae similar in form to those of *P. triarticulatus,* but with posterior portion of scaphognathite more slender. First maxilliped with curvature of endite less uniform; exopodite bearing laterally a heavy setiferous bristle (broken in specimens); epipodites greatly reduced. Second maxilliped with endopod composed of only three conspicuous articles, one being very short and sandwiched between the first and third; basal article more rectilinear than that of *P. triarticulatus;* penultimate article pear-shaped in outline, about 1.3 times as long as maximum breadth, bearing numerous heavy spines; tip half-round in outline, bearing six strong spines. Third maxillipeds similar in conformation to those of *P. triarticulatus* but with all three articles of endopod bearing heavy setae, the setae of last article being equal in length to article.

First legs lacking on both specimens. Carpus of second legs with four articles bearing the ratio 10:2.6:1.8:4.4; chela somewhat longer than distal carpal article, fingers and palm subequal. Third legs with ischium unarmed; merus 4 times as long as broad; carpus 0.9 as long as merus; propodus 1.2 times as long as merus, armed distally with few weak spines; dactylus biunguiculate.

Telson 2.1 times as long as posterior margin is broad, 1.2 times as broad anteriorly as posteriorly, lateral margins almost straight, posterior margin strongly arcuate; only one pair of dorsal spinules, located posterior to middle; inner pair of spines at posterior lateral margin half as long as posterior margin is broad. Only one tooth on basal article of uropod; distal shoulder of outer uropod armed with one strong lateral spine and three flanking spines each almost as long as lateral spine.

DISCUSSION: Even without the first legs, these specimens may be distinguished with ease from *P. triarticulatus.* Among more readily apparent differentiating characteristics, this species has (1) margins of the rostrum which are confluent with the anterior margin of the carapace;

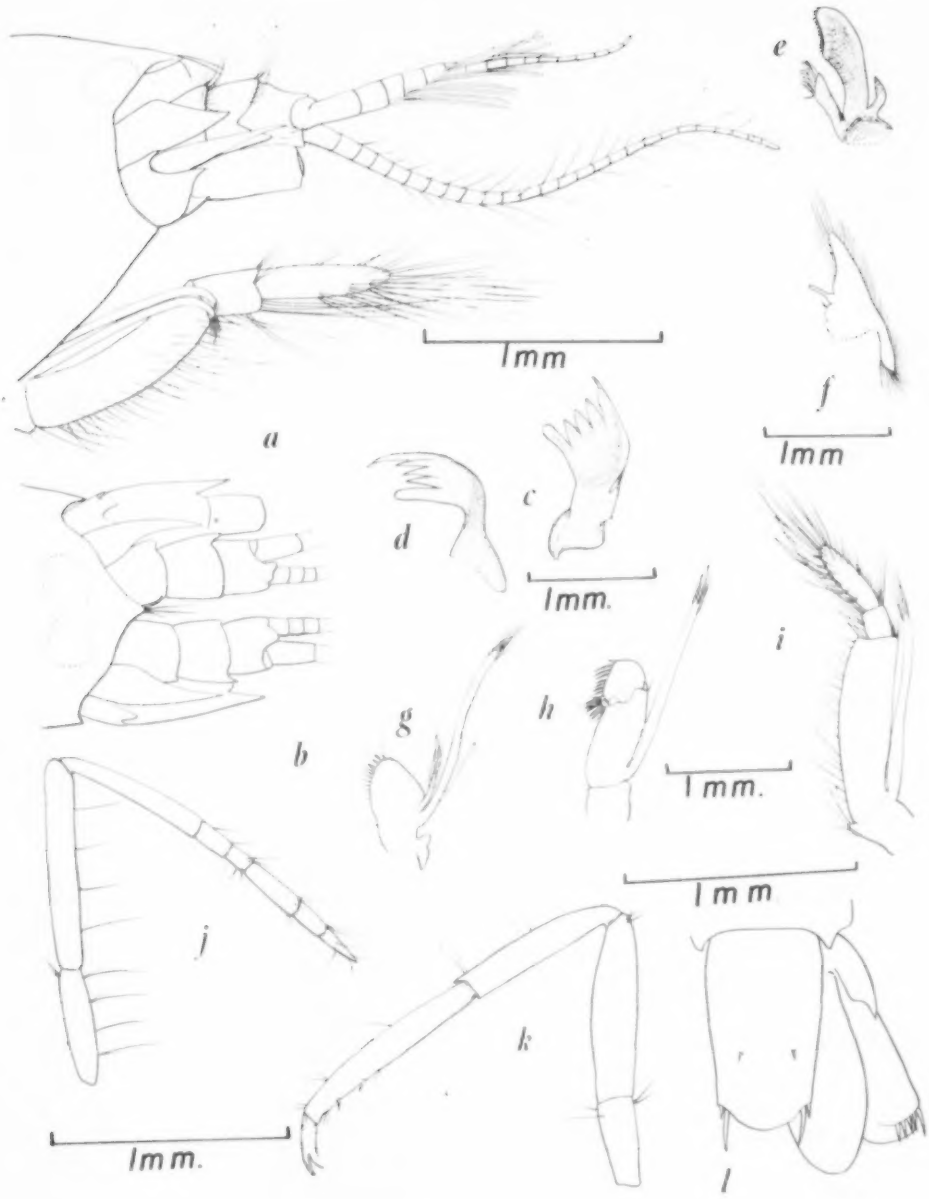

FIG. 2. *Prionalpheus* sp. *a, b.* Anterior body region; *c, d,* left mandible, median and posterior views; *e, f,* first and second maxillae; *g, h, i,* first, second, and third maxillipeds; *j,* second legs; *k,* third legs; *l,* telson and uropods.

(2) a pterygostomial angle which is less pronounced; (3) shorter scaphocerites and ventral lateral teeth of the basicerites; (4) more hirsute third maxillipeds; (5) four, rather than three, articles in the second legs; (6) a telson which has a different armature. In the mouth parts, the differences in form of the mandibles, the maxillulae, and the second maxillipeds are striking, as can be seen by comparing the figures. Whether the differences in length of the stylocerites, in the form of the third legs, and in the armature of the telson and uropods are significant cannot be determined without more specimens.

The species has been left unnamed because the specimens are so incomplete.

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Contributions to the Knowledge of the Alpheid Shrimp of the Pacific Ocean

Part VII. On *Metabetaeus* Borradaile, with a New Species from Hawaii[1]

ALBERT H. BANNER and DORA MAY BANNER[2]

THE GENUS *Metabetaeus* was described by Borradaile (1898: 1014) to contain the species originally described by Whitelegge (1897: 147) as *Betaeus minutus*. These descriptions and Coutière's subsequent discussion of the genus (1899: 374) were all based on a series of specimens collected at Funafuti in the Ellice Archipelago. Nothing more on either the genus or the species was recorded until R. W. Hiatt collected additional specimens of the species in a brackish pond at Arno in the Marshall Islands (Banner, 1957: 193).

Since the publication of the 1957 paper, additional specimens belonging to this genus have been observed alive and collected. *M. minutus* was taken from two different islets on Jaluit in the Marshall Islands during a trip in April, 1958, to observe typhoon damage on that atoll. The trip was sponsored by the Office of Naval Research, the Pacific Science Board, and the Bernice P. Bishop Museum.

More interesting is a new species of the genus collected from one locality on the island of Hawaii. The first several specimens came to us from the collections of the Bishop Museum; they had been collected in a pool in the Ka'u district of Hawaii by E. H. Bryan, Jr., Marian Kelly, and William Meinecke. In February, 1958, we collected more specimens from this pool. Many other pools, both in the Ka'u district and in other areas on other islands, were investigated, but no more specimens of this species were seen.

This study was supported in part by the National Science Foundation Grant NSFG–3863. The authors wish to express their appreciation to Mr. William Meinecke, who guided them to the pool and aided in the capture of the specimens.

Metabetaeus lohena sp. nov.
Fig. 1

SPECIMENS: Type specimen, an ovigerous female 16.6 mm. long; paratypes, 5 specimens collected by the authors and 4 other specimens collected by Bryan, Kelly, and Meinecke.

TYPE LOCALITY: All specimens came from a pool in the base of the rock known to the Hawaiians as Lohena, a few hundred yards from shore between the deserted villages of Wai-o-ahu-kini and Ka'ili-ki'i, immediately west of Ka Lae or South Point on Hawaii. Lohena is a rock perhaps a hundred or more feet in diameter surrounded by the boulders of an a'a lava flow; in its base are several fissures, one of which is a cave about 30 ft. long, 10 or 12 ft. wide at the mouth and 15–20 ft. high; the pool of brackish water is 4–6 ft. deep in the bottom of the cave.

DESCRIPTION: Carapace rounded dorsally, without grooves or keels. Rostrum acute with tip reaching to middle of first antennular article; dorsal surface rounded, lateral margins posteriorly concave. Supraorbital spines acute, half as long as rostrum. Eyes completely concealed in dorsal and lateral aspects; pigmented portions of corneas greatly reduced. Pterygostomial margin rounded.

Cardiac notch wanting; pleura of sixth abdominal somite articulated.

Second article of antennular peduncle as long as broad, shorter than visible portion of first, and longer than third article; flagella about as long as carapace. Stylocerite acute, with tip reaching to end of first antennular article.

Basicerite with strong, acute tooth below articulation of scaphocerite. Scaphocerite with

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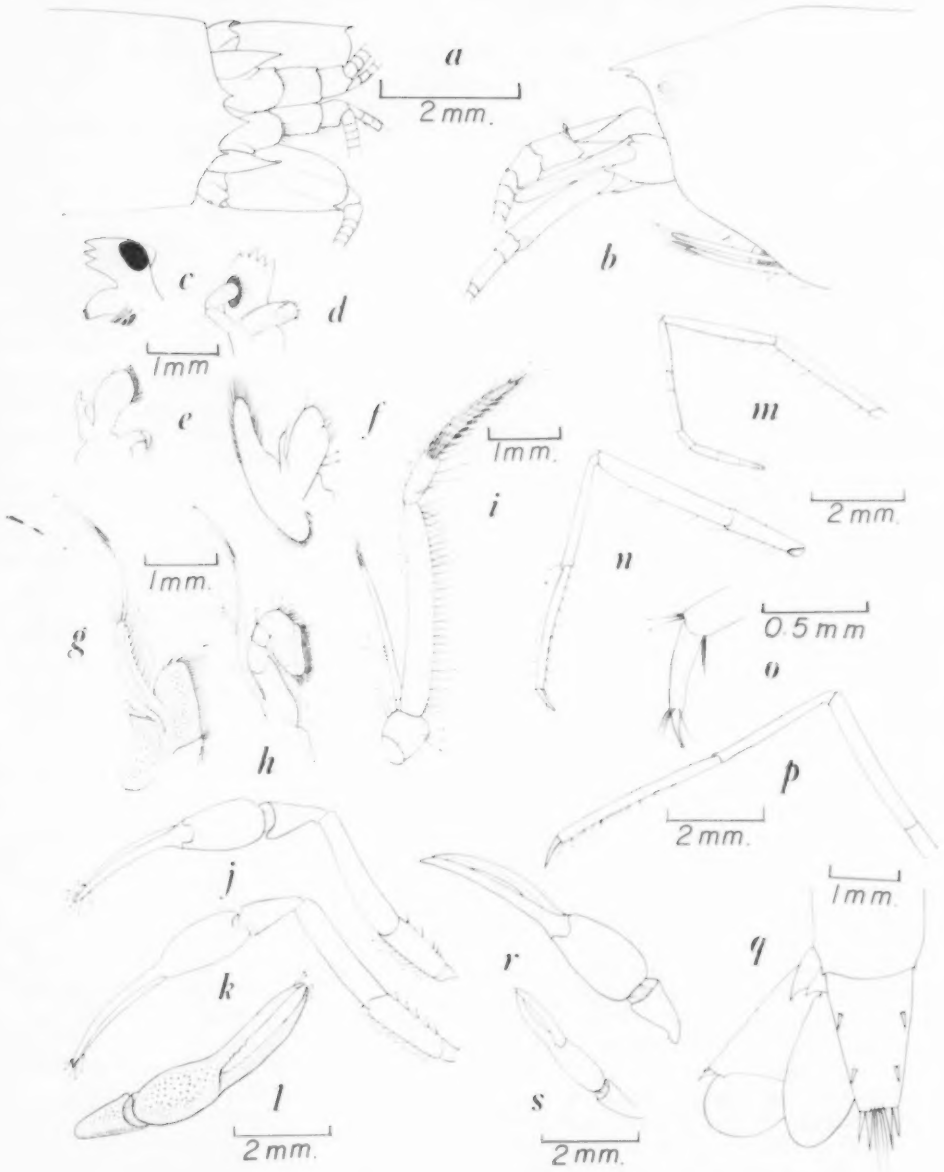

FIG. 1. *Metabetaeus lohena* Banner. *a, b*, Anterior region, dorsal and lateral aspects; *c, d*, mandibles; *e*, first maxilla; *f*, second maxilla; *g*, first maxilliped; *h*, second maxilliped; *i*, third maxilliped; *j*, left chela, outer side; *k*, right chela, inner side; *l*, left chela, upper side; *m*, second leg; *n*, third leg; *o*, dactylus, third leg; *p*, fifth leg; *q*, telson and uropods; *r, s*, paired chelae of a nonovigerous 18.4 mm. female.

lateral tooth of moderate development, about equal in length to rounded portion; squamous portion reaching to end of antennular peduncle. Carpocerite slightly longer than both antennular peduncle and scaphocerite; flagellum somewhat longer than body.

Mandibles of normal form but bearing a large oval black spot on the body of the mandible; black spot with sharp margins and persistent even after preservation in alcohol. Maxillule with outer lobe without setae or spines, but with two heavy, thickened lobes, somewhat similar in form to a bottle opener. Other mouth parts showing only minor differences from those normal to the family.

Chelipeds symmetrical, enlarged. Ischium 3 times as long as broad, bearing on superior margin a row of short spines, on inferior margin a row of setae. Merus unarmed, 5 times as long as broad, slightly over twice length of ischium. Carpus subconical, proximally small in diameter, distally 3 times the proximal diameter; distal margins somewhat collarlike around base of propodus; articles without spines. Palm of chela somewhat inflated, subcircular in cross section, 1.6 times as wide at maximum diameter as long. Fingers long, slender, curved, 1.5 times length of palm; proximally both fingers armed with low, widely spaced teeth.

Second legs long and slender, ischium and merus equal in length and both about 10 times as long as broad. Sum of lengths of first three carpal articles equal in length to merus; ratio of the carpal articles is 10:3.5:8:3.5:5. Fingers of chela subequal in length to last carpal article, slightly longer than palm.

Third legs slender. Ischium unarmed, except for scattered setae, almost 4 times as long as broad. Carpus unarmed, 0.8 as long as merus, about 0.6 as broad. Propodus also slender, slightly curved, tapering very slightly distally, 1.1 times as long as carpus, and bearing 10 slender, fine spines along inferior margin. Dactylus simple, slender, acute, 0.2 as long as propodus.

Fourth and fifth legs similar to, but progressively longer, than third. "Brush" on propodus of fifth legs well developed.

Telson twice as broad at base as at tip, and 3 times as long as broad at tip; lateral and terminal margins almost straight; dorsal surface slightly convex. Spines heavy with medial pair of terminal spines about as long as tip is broad; lateral pair slightly shorter; middle portion of tip with small tuft of plumose setae. Uropods normal in form, lateral spine of outer branch strong.

Color in life from a brilliant to a pale salmon red, with the black mandibular spot conspicuous.

DISCUSSION: These specimens show a variation in the form of the chelipeds reminiscent of the species of *Athanas*. Mature males and females have chelae as described above; slightly smaller specimens of both sexes have a large and a small chela (Fig. 1*r*, *s*); small specimens have both chelae similar to the smaller one of the asymmetrical pair. No other marked variation was noted with sex or maturity.

The differences between this species and *M. minutus* are few but conspicuous (contrast Fig. 1 and Fig. 2). The stylocerite of *M. lobena* reaches to the end of the first antennular article, that of *M. minutus* to the middle of the second; the scaphocerite reaches to the end of the antennular peduncle on this species, to the middle of the third article on *M. minutus*. More important are the differences in the chelae, with none of the numerous specimens of *M. minutus* showing the enlarged chelae; and with the fingers in all definitely shorter than the palm, while in *M. lobena* both the large and small type of chela have fingers longer than the palm; also, in *M. minutus* the fingers are quite straight and heavy, while in *M. lobena* the fingers are slender and show at least some curvature. Another possible difference is the degree of coverage of the eyes, with the eyes completely concealed in all specimens of *M. lobena*, and with them usually protruding in some degree from under the carapace in *M. minutus;* however, as the eyes may be rolled forward and backward, this characteristic should not be relied upon. There are no other conspicuous differences in the morphology of the two species. The color in life of the two species, including the black mandibular spot, is the same.

They are also similar in their environments. The habitat of *M. lobena* is described above; while surface layers of the water in the undisturbed pond were almost fresh, the under layers

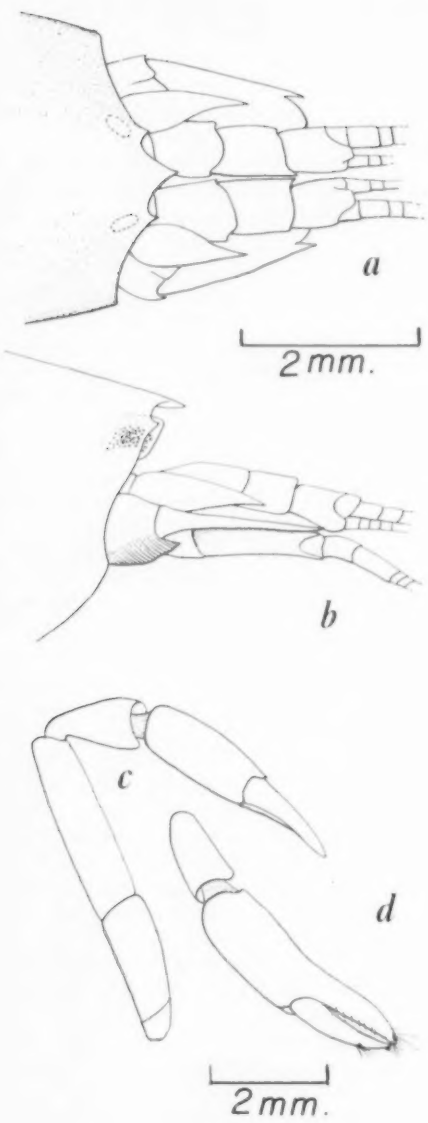

FIG. 2. *Metabetaeus minutus* (Whitelegge). *a, b*, Anterior region, dorsal and lateral aspects; *c*, cheliped; *d*, chela, outer face.

were definitely brackish, and the level of the water in the pool changed with the tides.

M. minutus was collected in two pools on Jaluit. On the islet of Medyado it was found in a mangrove swamp; the base of this swamp was an old reef flat, cut off from both the ocean and the lagoon by boulder and sand ramparts, and through the coral platform flowed definitely brackish water, rising and lowering not only with the tide but also with rapid periodicity of the waves on the ocean reef. The water flowed in and out through a series of ragged holes, and it was in these holes that the shrimp hid, emerging to the surrounding pools when unmolested. On Jabor the shrimp were found in a bomb crater in the center of the islet; the crater was almost dry at low tide and the shrimp were withdrawn into the holes of the coral at the base; but at high tide, when it was almost waist deep with brackish water, the shrimp emerged in great numbers.

However, in the ecology of the pools the two species appear to play entirely different roles. In the pool of Lohena there were two species of shrimp found; the smaller and much more abundant atyid was identified by Rathbun (1906: 919) as *Caridina brevirostris* Stimpson and the larger as *Metabetaeus*. The atyid, abundant in pools of subterranean origin about the Hawaiian Islands, is an herbivore evidently feeding upon the algae growing on the rocks of the pools and upon vegetable detritus falling into the pool. When undisturbed it settles in large numbers on rock surfaces, occasionally walking or swimming from rock to rock. The alpheid, about twice the size of the atyid, usually hides in the rubble at the bottom of the pool, or in cracks in its side, and makes sudden forays to capture the atyid in its long rapacious chelae. It carries the struggling atyid in its chela towards its mouth and disappears again into a hiding place, presumably to eat its prey.

On the other hand, while in the pools of Jaluit there was also an atyid (not as yet identified); the mature atyid and alpheid were of nearly the same size, and the alpheid was by far the more abundant and gave no evidence of predatory habits. Like the *Caridina* in Hawaiian pools, *M. minutus* would emerge to rest on the rocks and vegetable debris in the pool;

they were never seen attacking other shrimp. When the senior author stood bare-legged in the pool while collecting, shrimp settled on his leg and produced a feeling similar to a gentle rasping rather than pinching. In the food groove between the bases of the thoracic legs and among other mouth parts were found sand and detritus. Therefore, they are presumed to be other than carnivorous.

Coutière remarked that in his specimens of *M. minutus* there were spots similar in color to the mandibular spots found about the gill chambers and other parts; he suggested that they were caused by symbiotic zooxanthellae. In none of these specimens of either species were there spots other than the mandibular spots and the normal red chromatophores; moreover, in view of the habit of these shrimp, of living in darkness or semidarkness, it is unlikely that they would have an association with symbiotic algae.

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Localization and Proof of Chitin in the Opisthobranch Mollusks *Aplysia californica* Cooper and *Bulla gouldiana* (Pilsbry), with an Enzymochromatographic Method for Chitin Demonstration

LINDSAY R. WINKLER[1]

CHITIN HAS been generally considered as almost synonymous with the arthropod exoskeleton. However, as Richards (1951) points out, other substances enter into the structure of the arthropod exoskeleton and, conversely, some arthropods are known which have no detectable chitin. It is also true that chitin is found in other invertebrate phyla and in the plant kingdom as well. Wester (1909) and Kunike (1925) surveyed the animal kingdom for chitin and reported it present in at least some part of the body of members of most of the phyla below the echinoderms. These and the other authors mentioned below found chitin present in four of the five molluscan orders (Scaphopoda was not studied). Besides these works Sollas (1907), Spek (1919), Pantin (1925), and Tóth (1940) have contributed to the study of chitin in the Gastropoda. Chitin has been reported present in only two structures, the radula and the jaws. Tóth (1940) reported that the organic portion of the shell of *Helix pomatia* did not contain chitin. Kunike (1925) found no chitin in the organic shells of the gastropods and lamellibranchs which he tested. Roche (1951) hydrolyzed the organic residues of the gastropod shells of *Turbo, Meleagrina,* and two species of *Pinna,* and reported them to be scleroproteins. Spek tested the radulae and jaws of a number of common prosobranchs and pulmonates and of the opisthobranch *Aplysia* sp., and found chitin present in all cases. The radulae and jaws of the genera which have been tested in these works include *Helix, Arion, Patella, Haliotis, Natica, Conus, Buccinium, Littorina, Tergipes,* and *Aplysia.*

As Richards (1951) points out, it is essential that we establish a criterion for the demonstration of the polysaccharide chitin. He accepted a positive chitosan color test as the most valid qualitative test for the presence of chitin. This test is also the standard used in this paper, although the chromatographic demonstration of N-acetylglucosamine, the basic saccharide of chitin, would also be an adequate demonstration of the presence of chitin.

Besides the two chitinous structures previously studied, the opisthobranch *Aplysia,* commonly known as the sea hare, possesses two other "chitinous" structures, the stomach teeth and a vestigial shell, both of which are composed almost entirely of organic material. The shell-bearing opisthobranch, *Bulla,* possesses stomach teeth and a small amount of organic periostracum on its shell. These structures have been tested by the chitosan color test method. In addition, an enzymochromatographic method for chitin demonstration was adapted and tested and is herewith presented. The shell of the prosobranch *Oncomelania* was also tested for comparison.

MATERIALS AND METHODS

Stomach teeth were excised from growing specimens of *Aplysia californica* Cooper and frozen until ready for testing. Shells of adult specimens were removed and preserved in 70 per cent ethyl alcohol until tested.

Adult specimens of the shell-bearing opisthobranch, *Bulla gouldiana* (Pilsbry), were collected and preserved in neutral formalin (which was later changed to 70 per cent ethyl alcohol). When the test was made the shells were decalcified in 10 per cent HCl, rinsed well, and blotted. The dry shells of *Oncomelania nosophora* (Robson) were similarly decalcified.

[1] School of Tropical and Preventive Medicine, Loma Linda, California. Manuscript received January 2, 1959.

The difference in preparation was a result of convenience. Commerically prepared chitin was used for controls in all cases.

The chitosan color test of Campbell, as adapted by Richards (1951), was used as follows:

The chitin to be tested was placed in a test tube and a saturate solution of KOH was added. The tube was closed with a Bunsen valve (a piece of rubber tubing sealed at one end with a clamp and having a longitudinal slit 0.5–0 cm. long made on its lateral surface). The test tube was then placed in a glycerine bath and heated to 160° C. over a period of 15–20 min. It was held at this temperature for about 15 min. and allowed to cool to room temperature. The persistent material assumed to be chitosan[2] was then rinsed and divided for the following tests:

(1) Lugol's iodine was added, resulting in a brown color when positive. The excess iodine was removed and replaced with 1 per cent sulfuric acid. When chitin was present it changed color to what appeared black. However, upon mashing the specimen under a microscope, the true color—a reddish purple—was apparent (the chitosan color test). Adding 75 per cent sulfuric acid resulted in an immediate change to brown, followed by an eventual disappearance of the color as the material passed slowly into solution. (2) Three per cent acetic acid was added to another portion of the original KOH persistent material. When positive the tested substance passed slowly into solution. Addition of a drop of 1 per cent sulfuric acid then gave a white precipitate.

For the enzymochromatographic determination the chitin was mashed in a mortar or minced and placed in a miniature test tube. To this 1 ml. of snail enzyme preparation was added, after which it was incubated overnight at room temperature. After incubation small samples were applied in spots about 1½ in. apart on a line ½ in. from the base of 8 × 8-in. squares of Whatman No. 1 chromatographic paper. The paper was then formed into a cylinder and fastened with staples so that the base line described the circumference at one end. This end was then placed in a Petri dish containing water–saturated phenol (Mallinckrodt liquid) which was not deep enough to reach the sample. This in turn was placed in a 10-gal. aquarium and covered with a glass plate. When development was completed the paper was dried overnight and then washed in ether to remove all the phenol possible. After further drying the chromatogram was dipped in benzidine-trichloroacetic acid reagent and heated at 100° C. for about 15 min., or until the brown spots indicating reducing substances had thoroughly formed. The spots disappear after a few days so it is necessary to mark the spots and soak the papers in water to have a permanent record.

The snail enzyme reagent was prepared by excising the digestive gland of the common garden snail, *Helix aspersa*, and macerating it in a mortar with sand and acetate buffer at pH 5.2. It was then centrifuged and the liquid was used in the digestion as described.

The benzidine-tricholoracetic acid reagent was made as follows: 0.5 gm. of benzidine was dissolved in 5 ml. of glacial acetic acid and added to 4 gm. of trichloroacetic acid dissolved in 5 ml. of water. To this was added 90 ml. of acetone. If refrigerated it keeps about 2 weeks.

EXPERIMENTAL RESULTS

Both the nuclear area of the shell and the stomach teeth of *Aplysia californica* were resistant to the action of the hot alkali and gave very strong chitosan color tests. The confirmatory tests mentioned were also positive. The organic periostracum of *Bulla* contained small amounts of chitin although the major portion was not persistent. The stomach teeth of *Bulla* were composed principally of chitin. The decalcified organic shell of *Oncomelania*, however, did not withstand the action of the hot alkali. Some white powder released was tested but gave no color. This latter shell material was completely resistant to the snail enzymes.

Chromatographic spots at Rf .34 for all specimens and controls involving the snail enzyme preparation were the result of free sugars in the enzyme extract. The additional spots at an Rf value of approximately .69 appeared only in the aplysiid material tested and the chitin con-

[2] Few organic substances other than chitin can resist the KOH treatment.

trols. These represent the spots resulting from the presence of N-acetylglucosamine, the building block of chitin.

DISCUSSION AND CONCLUSION

The presence of chitin as the principal constituent of the stomach teeth may not be surprising, considering that the hard structures of the anterior digestive tract of all gastropods tested have been shown to consist of chitin. However, the organic portion of the gastropod shell has consistently been reported negative for chitin in other snail groups tested and has been found so in this investigation in the amphibious prosobranch *Oncomelania*. The nature of the shell and the relative proportions of calcium and organic matter are very different in the gastropods possessing calcareous shells as against the largely organic, vestigial shell of most opisthobranchs. At most the amount of organic matter in the calcareous type of shell of the former constitutes a periostracum or matrix. However, in many of the latter the vestigial shell is almost, if not entirely, composed of organic material. In the shell-bearing opisthobranch, *Bulla*, the organic matter is considerably less than in *Aplysia* and can be compared to that of the pulmonates, such as *Helix* and *Vivaparus*. The amount of calcium present in the aplysiid shell varies, some possessing little, if any, apparent calcareous layer, while in others a calcareous film or crust is formed on the inner surface of the organic shell. In *A. californica* rarely more than a translucent film is present. The presence of an occasional thicker calcareous layer in this latter species seems to be associated with a diet high in *Corallina* sp., a calcareous alga. Some species are said to normally deposit a calcareous layer or crust.

The enzymochromatographic method of chitin detection here adapted from existing techniques offers one very distinct advantage. As suggested by Richards (1951), there may be chitins in a broader sense which are not persistent in the hot KOH treatment used in the chitosan color test and therefore are not detected even though they are made up of the requisite N-acetylglucosamine. These would be detected by the enzymochromatographic method described unless they are not attacked by the snail enzyme—which is unlikely.

The presence of chitinase in the digestive gland of the large European snail, *Helix pomatia*, has been exploited in the past for the enzymatic dissolution of chitin (Karrer, 1930). Jeuniaux (1954) found a chitinase present in the digestive organs of *H. aspersa*, the common garden snail.

SUMMARY

The stomach teeth of *Aplysia californica* and *Bulla gouldiana* were tested for chitin by the specific chitosan color test method and were found to be strongly positive. The organic shell of *Aplysia californica* gave a positive chitosan and confirmatory test. The organic periostracum of *Bulla gouldiana* left some KOH-resistant material, giving positive chitosan color and confirmatory tests. The organic portion of the shell of the amphibious prosobranch, *Oncomelania*, was not KOH-resistant and was negative for chitin. The stomach teeth of *Aplysia* were tested by enzyme digestion, followed by chromatographic analysis of the soluble residues, and showed the presence of N-acetylglucosamine comparable to that found in the commercial chitin used as controls.

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Second Report on Hawaiian Polyclads

LIBBIE H. HYMAN[1]

THE MATERIAL of this report was kindly presented to me by Dr. C. E. Cutress. It adds slightly to our knowledge of the polyclad fauna of the Hawaiian Islands, reviewed in my previous report (Hyman, 1954). To the references given therein should be added Pease (1860), previously overlooked. Pease described and illustrated in color four polyclads from the Hawaiian Islands (exact location not stated); of these two are probably not identifiable.

The present specimens were collected under rocks in the intertidal zone at Makapuu Point, Oahu, in March, 1953.

ORDER POLYCLADIDA
SUBORDER ACOTYLEA
SECTION SCHEMATOMMATA
FAMILY PLANOCERIDAE

Paraplanocera oligoglena (Schmarda, 1859)

The occurrence of this almost circumtropical species in the Hawaiian Islands was previously recorded (Hyman, 1954: 333). The present specimen measures 28 by 21 mm. It is thin and ruffled; the color in life is described as tan or buff dotted with dark brown. There is little doubt that *Peasia reticulata* Pease (1860: 37) is identical with *Paraplanocera oligoglena*. Pease gives a recognizable colored figure (pl. 70, figs. 1, 2) and a colored figure also appears in Stummer-Traunfels (1933, col. pl. following p. 3596, fig. 6).

SUBORDER COTYLEA
FAMILY PSEUDOCERIDAE

Thysanozoon hawaiiensis, n. sp.
Fig. 1

The single specimen is of oval form and thin consistency, measuring 24 by 13 mm. The color in life was stated to be light ochre with dull-green papillae. At the center of the anterior margin are seen the usual pair of tentacular folds, bearing eyes. Behind them is a rounded cluster of cerebral eyes. This is followed by the ruffled pharynx of compact oval outline. Because of damage in the critical region, just behind the pharynx, it could not be determined whether the male apparatus is single or paired. The female gonopore and the sucker, located as shown in the figure, were readily noticeable. The sucker occurs at about half the length of

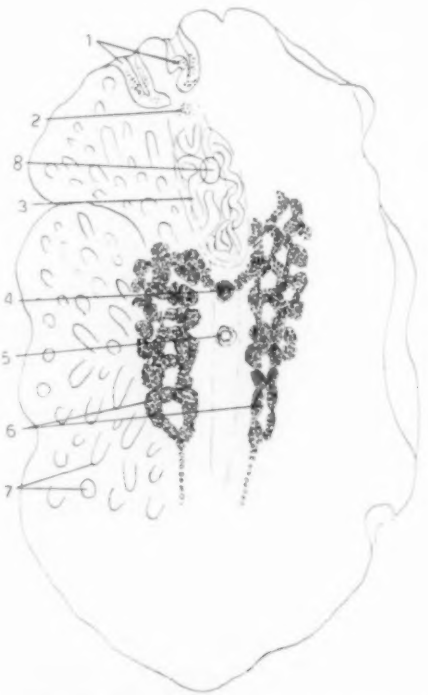

FIG. 1. *Thysanozoon hawaiiensis*. *1*, Tentacles; *2*, cerebral eye cluster; *3*, pharynx; *4*, female gonopore; *5*, sucker; *6*, uteri with eggs; *7*, papillae, shown in part only; *8*, mouth.

[1] American Museum of Natural History, New York, N. Y. Manuscript received January 26, 1959.

the animal. To either side in the middle region of the worm the brown uterine networks filled with eggs are conspicuous even to the naked eye. As typical of the genus the dorsal surface bears numerous papillae with rounded tips. They are only fairly numerous and not thickly set. They are not entered by a branch of the intestine.

It has been very difficult for me to decide whether the present species might not be identical with *Peasia tentaculata* (Pease, 1860: 37), which is obviously a species of *Thysanozoon*. Neither the description nor the colored figure (pl. 70, figs. 5, 6) are very helpful. The color is stated to be light fawn with darker papillae, agreeing well enough with the present specimen, but the red line around the margin does not agree. The papillae are depicted as pointed and described as mucronate, that is, suddenly narrowing to a pointed tip. The features of the ventral surface in Pease's figure are not understandable in terms of the genus. Because of these discrepancies I judge it preferable to consider my specimen an undescribed species.

The specimen in alcohol is deposited as a holotype in the Bishop Museum.

Pseudoceros affinis (Kelaart, 1858)

The specimen is of oval form, measuring 30 by 20 mm., with ruffled margins and typical tentacular folds at the anterior margin. The color is described by the collector as deep violet with a bright orange margin edged with black. The species has a pair of male apparatuses. The male gonopores occur at 12 mm. from the anterior margin, the female gonopore at 13.5 mm., and the sucker at 17.5 mm., hence situated considerably anterior to the middle. In addition to the colored figure in Collingwood (1876, pl. 19, fig. 23), there is a colored figure in Stummer-Traunfels (1933, col. pl. following p. 3596, fig. 11). This latter figure closely resembles my specimen.

Pseudoceros affinis is probably common in the tropical west Pacific. The original specimen came from Ceylon and the specimen in Stummer-Traunfels was part of the Semper material collected in the Philippines; the colored figure was made from life by Mrs. Semper. The present record from the Hawaiian Islands indicates an extensive range for the species.

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